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ASYMMETRIC COLOR RESEMBLANCE IN THE GUINEA PIG[1]

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As is well known, the guinea pig shows the greatest diversity of color, and a great diversity in distribution of color over the body of the animal. In the course of our experience with these animals in physiological and toxicological work we have seen pigs that were entirely black, others that were entirely brown, others of a pure albino variety, and more commonly than any of these pure color strains, those showing apparently every possible variation in the arrangement and distribution of these fundamental colors over the body. To what extent the color of the guinea pig and its variations as the result of the cross breeding of several strains of different colors have been the subject of exact scientific observation, we are unable to say, and the subject is so far removed from those ordinarily engaging our attention that it would take us too long to familiarize ourselves with this knowledge, particularly should it prove in any way extensive. In the course of some of our recent investigations, however, we have observed what seems to us to be a rather remarkable case of asymmetric color resemblance and distribution of color on the part of the daughter for the mother in the guinea pig, which is perhaps worthy of note to those more deeply interested in matters of this kind.

One of our female guinea pigs which has been under observation and experimentation for some time, No. 68, was aborted by means of calcium lactate[2] on March 29,

[1] From the Laboratory of the Kentucky Agricultural Experiment Station.

[2] Kastle and Healy, "Calcium Salts and the Onset of Labor," *Jour. of Infectious Diseases*, Vol. X, 1912, 378–382.

1912. No bad effects resulted from the abortion and the pig soon regained her normal condition and was returned to the piggery on April 9, 1912. Shortly after this she again became pregnant and during the greater part of her pregnancy she was kept in a small cage with another female pig as one of a set of pigs employed in the study of the calcium metabolism of the guinea pig.[3] At the conclusion of these observations she was again returned to the piggery on June 13, 1912, and on June 24, 1912, she was again brought back to the laboratory. During the day she gave normal birth to three pigs, weighing respectively 40, 40.5 and 43.5 grams. One of these young pigs was dead when examined a few hours after birth, the other two were alive. Of the latter, one was paralyzed in its hind quarters and died, probably of inanition, a few days after birth. The remaining pig, a female, was normal in every respect and is alive and well to-day (August 5, 1912), and now weighs 157 grams. It was observed by Dr. Buckner that the color markings on the young pig are like those on the mother, except that these markings are on exactly opposite positions on the body. In other words, these two pigs, mother and daughter, show an asymmetric color resemblance. That such is the case is evident from the photographs, Figs, 1, 2, 3 and 4, although these fail to show this as well as the originals for the reason that the actual colors are wanting. Furthermore, this remarkable resemblance is a little obscured and marred by the fact that the young pig has considerably longer hair than the mother, probably as the result of an Angora strain. Unfortunately, too, nothing is known regarding the parentage of this pig on the male side. The following is an exact description of the two pigs, which in order to render comparisons more easy, is printed in double columns and given for opposite portions of the body, in order to bring out the asymmetric character of the resemblance.

MOTHER PIG	YOUNG PIG (FEMALE)
The mother pig is 9 inches long from tip of tail to tip of nose and	The young pig is 6 inches long, and 2½ inches wide across widest part

[3] Kastle, Healy and Shedd, "Calcium in its Relation to Anaphylaxis" (in press).

3½ inches in width across widest part of body. Weight 570 grams. (August 5, 1912.)	of body. Weight 157 grams. (August 5, 1912.)
Right cheek and area surrounding right eye, light tan.	Left cheek and area surrounding left eye, light tan.
Mouth, nose and middle of forehead white, the white area on forehead narrowing somewhat just behind the middle of ears and then broadening out over shoulders and upper part of back and then gradually giving place to light tan in the middle or rear portion of back.	Mouth, nose and middle of forehead white, the white area on forehead narrowing somewhat just between the ears and then extends backward over shoulders, broadening somewhat over upper part of back.
Right ear an intimate mixture of black and tan, giving the impression at first glance of black.	Left ear is covered, especially towards the front with a mixture of black and tan, with a small amount of white hair immediately in front and under ear.
The greater part of the right side is almost pure light tan, darkening somewhat towards and over the back, and at a point immediately back of the fore-shoulder there is a narrow white band extending from the white area over the shoulder to a point where the front leg joins the body.	The greater part of the left side of this pig from a point about the front of shoulder to a point near the hip is entirely light tan, with exception of a rather well-marked band of white, which looks almost like a white collar on the left side of the pig near the shoulder, and which is broader and more well-developed than in the mother.
The right front leg is light tan with the exception of the upper part of the foot which is white.	The left front leg is light tan extending down to foot, the top of which is white.
The inside of right ankle and foot is nearly hairless and shows a well-defined black spot in the skin.	The inside of the left ankle and foot is nearly hairless and shows a well-defined black spot in the skin.
Left fore foot, left fore leg and left side, including left hind leg entirely white, with the exception of a small area of light tan over the middle and rear portion of back.	Right fore foot, right fore leg, and right side, including right hind leg entirely white, with the exception of a small area of light tan, over the middle and rear portion of back.
Under part of mouth and under jaw, extending down over left fore leg white. The abdominal portion of the body is white including the hind legs, except a portion of the right side of the chest which is very light tan.	Under part of mouth and under jaw, extending down over right fore leg white. The abdominal portion of the body, including the hind legs is white, except a portion of left side of the chest which is light tan.
Left ear is nearly hairless and white.	Right ear is nearly hairless and

with a small area of tan extending over the front of ear.	white, with a small area of tan extending over the front of ear.
Rump entirely white.	Rump entirely white.
Eyes black.	Eyes black.
Left cheek and area surrounding left eye is tan, extending to left ear.	Right cheek and area surrounding right eye is tan, extending back to ear.

It will be observed from a careful examination of the photographs, Figs. 1, 2, 3 and 4, that these pigs show certain minor differences in color distribution over the body. These are due in part at least to the fact that the

FIG. 1.

hair of the young pig is considerably longer than that of the mother—the latter being a smooth haired pig, whereas the former shows an Angora strain. Thus it will be seen from Fig. 1, that the small patch of white hair over the left eye of the young pig is larger than the corresponding patch of white over the right eye of the mother, otherwise the asymmetric resemblances shown in the front view of the two pigs is essentially perfect, barring the somewhat longer hair of the young pig. In Fig. 2, the white band extending around the left fore shoulder of the young pig is decidedly wider and more evenly distributed than the white marking over the right shoulder of the mother. This is doubtless due in part to the fact that the hair of the young pig is longer and consequently overlaps

the tan-colored hair immediately back of the white area. It will also be observed that in the young pig there is a narrow strip of white hair surrounding the lower margin of the left ear, whereas in the mother such a marking is not shown in the corresponding area of the right ear.

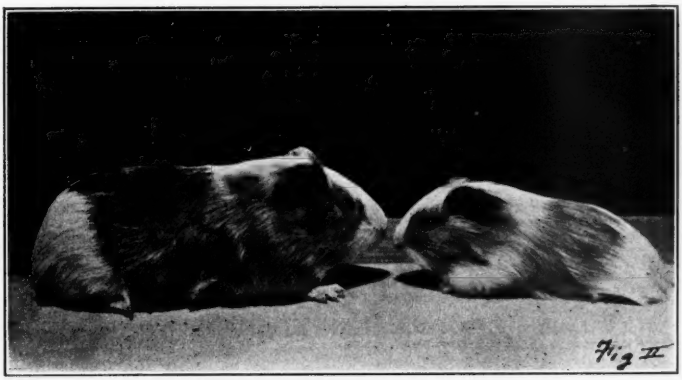

FIG. 2.

Here again this difference in the photograph, Fig. 2, is accentuated by reason of the longer hair of the young animal.

In Fig. 3 we certainly have a beautiful illustration of the asymmetric distribution of color in these two guinea pigs, the only points of difference being a very small area of white hair immediately under the left ear of the mother that is not apparent under the right ear of the young pig; and also a carrying forward of the tan area nearer to the mouth on the right cheek of the young pig than on the left cheek of the mother.

Fig. 4 also serves to show the asymmetric color resemblance in these pigs, somewhat imperfectly, however, on account of the partial disarrangement of a portion of the long tan-colored hair of the small pig. Hence we note, in Fig. 4, a slight extension of the white area into the darker area on the back of the small pig. As a matter of fact, however, a careful examination of the animals showed a perfect asymmetric resemblance so far as distribution of color is concerned, when looked at from the back. This could doubtless be brought out by other photographs, but

it is difficult to obtain good photographs of guinea pigs in all positions on account of their nervousness.

Despite these minor differences in color distribution over the bodies of the young pig and its mother, there

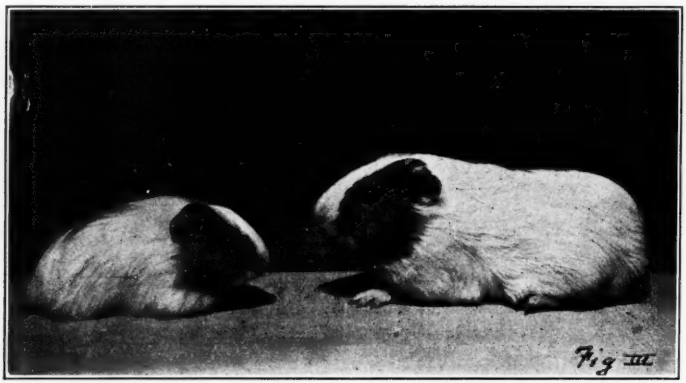

FIG. 3.

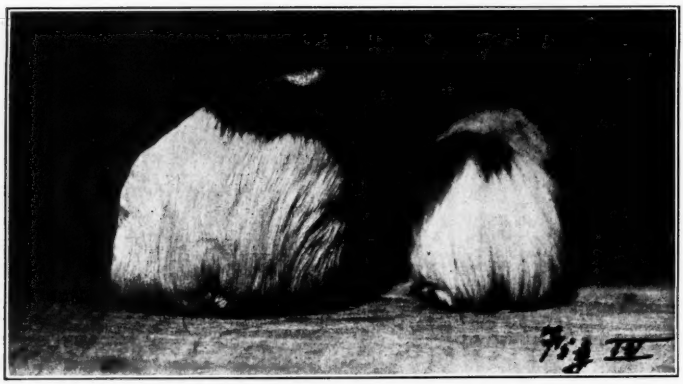

FIG. 4.

can be no question that we have here a remarkable case of asymmetric color resemblance between this female guinea pig and one of her offspring. It would seem further that this asymmetric resemblance and distribution of color in the young pig as compared with the mother is a characteristic inherited from the mother. Unfortunately, as has already been pointed out, nothing is known as to the

parentage of the young pig on the male side, and no record was kept of the color of the other two pigs of this litter, for the reason that this peculiar resemblance between this pig and the mother had not been observed at the time that the other two pigs of the same litter died. Our recollection is, however, that the pig of this litter that was born dead was pure tan, whereas the one whose hind quarters were paralyzed and that died a few days after birth was white with tan and black markings. So far as we can recall, however, these markings were altogether different in arrangement and distribution from those of the mother.

To the chemist the matter of asymmetry as affecting the physical and chemical properties of certain chemical compounds, especially those containing carbon, and as applied to the constitution of such compounds, has since the memorable researches of Pasteur on the tartaric acids and the later work of Le Bel and Van't Hoff, been a particularly fruitful field for observation and research. It is also a matter of interest to observe in this connection that the character of the asymmetry shown by certain compounds of carbon greatly influences their assimilability by the lower plants. To what extent asymmetric conditions hold in the ovum and germ-cell we have no means of determining at present, and as already indicated in the foregoing, it is a subject which takes us too far afield from matters ordinarily engaging our attention. We have reason to believe, however, that asymmetric color resemblance in animals such as has been described in the foregoing, is rare and from the point of view of the chemist, extremely interesting and suggestive, and affords a subject which, in our opinion, would probably repay a more extended study on the part of those interested in animal breeding and the study of inherited characteristics.

In conclusion, we desire to express our thanks to Mr. T. R. Bryant, of the Station Staff, for his kindness in making the photographs used in the illustration of this article.

ON DIFFERENTIAL MORTALITY WITH RESPECT TO SEED WEIGHT OCCURRING IN FIELD CULTURES OF PHASEOLUS VULGARIS

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INTRODUCTORY REMARKS

IN the rather voluminous literature of seed testing, comparatively little attention has been given to the possible relationship between the characteristics of the seed (or of the plant from which it was gathered) and its viability. This is of course attributable to the fact that such work has been done chiefly for immediately practical ends, the object being in most cases to determine, by germination tests of a small sample, the suitability of a given bulk of seed for commercial planting.

To the student of natural selection, however, the cardinal problem of viability is to determine whether the capacity for development of a seed is a function of its patent or potential (*i. e.*, of its own measurable or of its inherent but as yet undeveloped) characteristics. A satisfactory solution of this very complicated problem would, I believe, be of rather wide interest. At the outset, however, one must fix clearly in mind that if a selective mortality be demonstrated, it has no necessary bearing upon the question of the origin of species. Natural selection may maintain a type already differentiated as well as mould new forms but in order to do either the variations upon which it acts must be heritable. But in any case the results would be of interest to the physiologist concerned with the problems of the relationship between form and function. Finally, exact information on the relationship between structural characteristics and viability—if they exist—may be of some practical importance in agriculture and plant breeding.

The purpose of this paper is to present the first results of a series of studies on the relationship between the structural characteristics of the parent plant or of the seed itself and its viability. The data here recorded relate only to seed weight and are drawn from an extensive series of field plantings of carefully selected and individually weighed seeds of the common bean, *Phaseolus vulgaris*. They are properly described as a by-product, for the experiments were not carried out especially nor in the most satisfactory manner to test the existence of a selective mortality.

The conditions in field cultures of individually labelled seeds are such that many factors besides the weight of the seed are concerned in determining whether or not a seed shall develop into a mature plant. Some are lost by dashing rains separating seeds and labels, after which all questionable cases have to be thrown away. Some are destroyed by rodents and some by the unavoidable accidents of cultivation. In natural selection terminology, the non-selective death rate—the death rate which is no function of the characteristics of the individual—is very high. This tends to obscure the selective death rate, if such exists.

For just these reasons, I have never taken account of the characteristics of the seeds which failed to develop into mature plants, although the desirability of testing for the existence of a selective mortality for seed weight has been in mind almost from the beginning of the breeding experiments with garden beans in 1907. The records of those which developed to maturity were available for studies of heredity, influence of size of seed planted on characteristics of the plants produced, and so on. Data for the entire parental population from which the seeds planted were drawn were at hand for the study of the influences of season and environment. Under these circumstances, the only need for a record of the seeds which failed to develop to maturity would be for testing the hypothesis of the existence of a selective death rate. As

suggested above, it seemed *a priori* improbable that a selective mortality could be detected in the large non-selective death rate of field cultures. But from an examination of the data which have accumulated during the last several years, it appears that the *a priori* scepticism which led to omitting records of the characteristics of the seeds failing to develop was unjustified. There appears to be, in fact, a selective mortality detectible by proper methods, even in field cultures.

The evidence upon which this statement is based is of the following kind. We know (*a*) the weight of all the seeds weighed in any year and (*b*) the weights of the sub-sample of seeds which developed into mature fertile plants in any subsequent year. Now the sample or samples which were planted were purely random drawings from the grand population forming the entire mass of seeds weighed for any culture. The physical constants for the distribution of weights of these sub-samples planted are, therefore, identical with those of the grand population, plus or minus the errors of random sampling. Ideally, to determine whether there be a differential mortality, we should compare the physical constants (means, standard deviations, and coefficients of variation) of the seeds which produced mature plants either with the constants of those of the same sub-samples which failed to do so or with the constants for the entire sub-sample planted. Practically, our end can be attained with reasonable exactness by comparing the constants of seeds which develop to maturity with those of the general population from which the plantings were drawn. The only objections to this procedure are two: (*a*) the results will be vitiated if the series of seeds planted are in any way selected, *i. e.*, not a purely random drawing from the general population, (*b*) the probable errors of random sampling in the drawing of the sample for planting are added to the probable errors of sampling due to the non-selective (purely random) death rate.

The first objection does not hold in the series discussed

here, for I am confident that the plantings were true random samples of the general population of seeds weighed. With regard to the second, we note merely that its influence will make the detection of a selective mortality more difficult. If we find indications that the chances for development of a seed are conditioned by its weight we must therefore consider that the influence of weight is probably even stronger than is indicated by our evidence. Indeed, there might be a selective death rate scarcely detectible by the methods necessarily used in this study, but if these methods do indicate a selective elimination, we may have considerable confidence in its reality.

Studies of viability are generally limited to the capacity for forming a growing seedling, but there is no reason why tests should not be made more stringent by extending them to the capacity of the embryo for developing into a fertile plant. This has been done in these experiments.

Presentation of Data

The seriations of weights of seeds for the general populations are given in Table I; those for the sub-series of seeds which actually developed into fertile plants in Table II. The seriations for the grand populations are designated by the key letters of the crops of plants which produced them, those for the viable sub-samples by the key letters of the crops into which they developed.[1] The weights are recorded in units of .025 gram range; class 1 being 0–.025 gram, class 2, .025–.050 gram, etc. The constants are also expressed in terms of these units, but any one desiring to do so may easily transmute them into fractions of grams.

The biometric constants for the grand populations are given in Table III. Those for the sub-samples which actually produced fertile plants appear in Table IV.

[1] These key letters are the same as those used in other papers published or in preparation. Hence, further information can be obtained by those who desire.

TABLE I

WEIGHT OF SEEDS FOR GENERAL POPULATION

Series	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	Totals
NH.....	2	2	14	87	361	1049	1507	1369	879	363	101	33	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5778
NHH...	—	—	5	37	251	989	1963	2071	1253	489	172	69	24	8	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7334
NHD...	3	13	92	408	1037	1766	1732	995	417	119	37	8	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6630
ND.....	1	28	108	339	733	681	317	126	24	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2362
NDD...	—	13	32	118	371	663	632	366	130	33	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2362
NDH...	1	1	8	72	335	883	976	647	242	50	10	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3227
US.....	—	—	1	1	1	4	22	44	163	343	448	431	341	188	124	80	72	54	43	15	9	6	1	—	—	—	—	—	—	—	—	2391
USH....	—	—	1	1	2	—	2	23	90	165	219	212	161	103	59	52	40	13	18	3	—	1	—	—	—	—	—	—	—	—	—	1165
USD....	—	—	2	8	25	75	153	224	205	151	81	50	15	8	2	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1002
FS.....	4	16	79	227	565	841	723	365	148	31	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3000
FSH....	1	1	12	52	262	742	698	275	61	16	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2122
FSD....	4	13	118	504	825	372	127	24	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1989
G.....	—	—	—	—	—	—	—	1	2	1	6	14	18	21	49	55	53	73	115	129	102	79	85	61	52	26	21	19	7	7	1	997
GG.....	—	—	1	3	4	25	36	74	137	220	383	523	689	919	1073	1016	923	784	612	390	250	161	80	38	14	5	3	1	—	—	—	8364
GGH...	—	—	—	1	—	—	—	3	1	14	41	74	123	229	330	461	423	374	307	201	114	67	36	11	10	3	3	2	—	—	—	2828
GGD...	—	—	1	1	2	7	12	36	75	157	298	377	368	294	194	127	91	52	25	9	7	5	2	—	—	—	—	—	—	—	—	2140
L.....	—	1	5	8	15	32	38	81	96	144	217	336	339	401	305	304	232	184	69	28	15	9	1	1	—	—	—	—	—	—	—	2861

TABLE II

Weight of Seeds Producing Fertile Plants

Series	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	Totals
NHD	1	—	3	18	89	276	386	298	211	95	28	8	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1416
NHH	—	1	3	23	96	281	401	330	216	94	25	9	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1484
NHHH	—	—	—	10	95	265	376	308	151	51	8	4	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1271
NHDD	2	3	14	80	230	319	285	157	80	25	6	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1204
NDH	1	8	26	76	198	209	104	37	9	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	670
NDD	—	3	25	53	143	151	87	42	8	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	513
NDDD	—	2	4	15	44	124	147	87	27	6	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	459
NDHH	1	—	1	13	42	160	164	130	42	9	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	565
US	—	—	—	—	—	—	8	18	57	118	124	117	79	43	34	19	23	16	13	6	3	2	—	—	—	—	—	—	—	—	—	680
USH	—	—	—	—	1	1	1	10	27	43	73	56	61	28	15	12	11	8	11	1	1	1	—	—	—	—	—	—	—	—	—	361
USD	—	—	—	—	—	—	5	3	16	48	55	60	53	19	14	9	12	8	3	4	1	2	—	—	—	—	—	—	—	—	—	312
USC	—	1	1	1	—	2	4	5	27	62	92	109	70	60	28	21	19	16	8	2	2	—	—	—	—	—	—	—	—	—	—	530
USHH	—	—	—	—	—	—	—	5	20	26	43	49	36	26	8	6	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	224
USDD	—	—	—	2	5	13	31	49	61	34	22	14	5	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	237
FSS	—	6	21	72	170	241	194	118	36	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	868
FSH	—	2	9	43	80	116	131	64	24	5	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	475
FSD	2	3	10	25	78	138	102	43	20	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	428
FSC	1	1	15	40	98	168	154	72	31	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	586
FSHH	—	1	3	13	43	166	131	60	10	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	429
FSDD	1	2	10	79	166	84	36	8	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	387
GG	—	—	—	—	—	—	—	1	1	1	3	9	14	17	36	44	37	57	82	96	81	63	64	54	43	18	16	13	4	4	1	759
GGH	—	—	—	1	—	1	3	6	8	23	25	38	40	65	79	49	56	70	46	33	22	9	5	3	1	—	—	—	—	—	—	583
GGH_2	—	—	—	—	—	2	6	2	9	8	19	37	53	56	76	56	56	50	31	19	8	5	2	2	1	1	—	—	—	—	—	499
GGD	—	—	—	—	—	—	2	3	8	16	31	33	42	58	64	52	64	44	38	35	9	7	5	2	1	—	—	—	—	—	—	514
GGD_2	—	—	—	—	—	1	—	4	8	12	24	28	39	41	64	59	65	35	31	17	10	8	1	2	—	—	—	—	—	—	—	449
GGHH	—	—	—	—	—	—	—	1	—	—	15	18	27	39	55	76	56	50	30	17	6	4	—	2	—	—	—	—	—	—	—	396
GGDD	—	—	—	—	1	1	2	3	5	16	38	49	61	57	45	24	21	11	5	1	2	—	—	—	—	—	—	—	—	—	—	342
LL	—	—	—	—	—	—	16	35	37	66	95	132	135	169	128	123	85	74	18	—	5	1	—	—	—	—	—	—	—	—	—	1141

TABLE III

BIOMETRIC CONSTANTS FOR GENERAL POPULATION OF SEEDS WEIGHED

Series	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
NH	9.474 ± .013	1.490 ± .009	15.727 ± .101
NHH	9.774 ± .011	1.421 ± .008	14.537 ± .082
NHD	8.529 ± .012	1.458 ± .009	17.099 ± .103
ND	7.496 ± .018	1.310 ± .013	17.470 ± .182
NDD	8.487 ± .019	1.377 ± .014	16.218 ± .163
NDH	8.852 ± .015	1.555 ± .011	14.089 ± .121
US	14.297 ± .036	2.605 ± .025	18.218 ± .184
USH	14.204 ± .047	2.413 ± .034	16.987 ± .244
USD	10.690 ± .041	1.921 ± .029	17.972 ± .279
FS	8.229 ± .018	1.434 ± .013	17.427 ± .156
FSH	8.516 ± .016	1.092 ± .011	12.826 ± .135
FSD	6.956 ± .016	1.034 ± .011	14.858 ± .161
G	22.272 ± .081	3.796 ± .057	17.044 ± .265
GG	17.601 ± .024	3.264 ± .017	18.542 ± .100
GGH	18.919 ± .034	2.674 ± .024	14.131 ± .177
GGD	14.972 ± .036	2.498 ± .026	16.681 ± .193
L	15.667 ± .040	3.137 ± .028	20.023 ± .186

TABLE IV

BIOMETRIC CONSTANTS FOR SEEDS WHICH PRODUCED FERTILE PLANTS

Series	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
NHD	9.458 ± .027	1.507 ± .019	15.932 ± .207
NHH	9.445 ± .026	1.508 ± .019	15.962 ± .203
NHHH	9.275 ± .025	1.332 ± .018	14.356 ± .196
NHDD	8.459 ± .027	1.409 ± .019	16.657 ± .235
NDH	7.624 ± .033	1.283 ± .024	16.833 ± .319
NDD	7.733 ± .039	1.318 ± .028	17.049 ± .369
NDDD	8.756 ± .041	1.304 ± .029	14.892 ± .339
NDHH	8.929 ± .035	1.244 ± .025	13.930 ± .285
USS	14.143 ± .070	2.713 ± .050	19.180 ± .364
USH	14.330 ± .094	2.650 ± .067	18.495 ± .480
USD	14.394 ± .101	2.632 ± .071	18.283 ± .510
USC	14.496 ± .076	2.583 ± .054	17.819 ± .381
USHH	13.942 ± .087	1.927 ± .061	13.820 ± .449
USDD	10.852 ± .078	1.777 ± .055	16.371 ± .521
FSS	8.204 ± .033	1.434 ± .023	17.478 ± .292
FSH	8.326 ± .045	1.438 ± .032	17.276 ± .389
FSD	8.224 ± .047	1.430 ± .033	17.383 ± .413
FSC	8.312 ± .039	1.397 ± .028	16.809 ± .340
FSHH	8.483 ± .035	1.075 ± .025	12.668 ± .296
FSDD	7.194 ± .036	1.045 ± .025	14.520 ± .359
GG	22.324 ± .091	3.727 ± .065	16.695 ± .297
GGH	17.659 ± .094	3.359 ± .066	19.020 ± .389
GGH_2	17.305 ± .093	3.079 ± .066	17.792 ± .392
GGD	17.545 ± .095	3.188 ± .067	18.168 ± .395
GGD_2	17.448 ± .096	3.023 ± .068	17.327 ± .402
GGHH	18.038 ± .083	2.445 ± .059	13.555 ± .331
GGDD	15.515 ± .088	2.410 ± .062	15.536 ± .410
LL	15.524 ± .059	2.968 ± .042	19.121 ± .280

in all cases. Only the deviations of the sub-samples from the general population, *i. e.*, the differences obtained by Sheppard's correction was applied to the second moment subtracting constants for the general population from those for the sub-samples producing fertile plants, as given in Table V, require our attention.

Consider first the differences in mean seed weight.

They are equally divided between positive and negative, the average weight of the seeds which produced fertile plants being in 14 cases higher and in 14 cases lower than that of the general population of seeds from which the plantings were made. The average value of the posi-

TABLE V

COMPARISON OF CONSTANTS FOR SEEDS PRODUCING FERTILE PLANTS WITH THOSE FOR THE GENERAL POPULATIONS WEIGHED

Series Compared	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
NHD–NH	−.016 ± .030	+.017 ± .021	+ .205 ± .230
NHH–NH	−.030 ± .030	+.018 ± .021	+ .235 ± .227
NHHH–NHH	−.500 ± .028	−.089 ± .020	− .181 ± .212
NHDD–NHD	−.070 ± .030	−.049 ± .021	− .442 ± .257
NDH–ND	+.128 ± .038	−.026 ± .027	− .637 ± .367
NDD–ND	+.237 ± .043	+.009 ± .031	− .421 ± .412
NDDD–NDD	+.269 ± .045	−.073 ± .032	−1.326 ± .376
NDHH–NDH	+.078 ± .038	−.312 ± .027	− .159 ± .310
USS–US	−.154 ± .025	+.108 ± .056	+ .962 ± .408
USH–US	+.033 ± .101	+.046 ± .071	+ .277 ± .514
USD–US	+.098 ± .107	+.027 ± .076	+ .064 ± .542
USC–US	+.200 ± .084	−.021 ± .059	− .399 ± .423
USHH–USH	−.262 ± .099	−.486 ± .070	−3.167 ± .511
USDD–USD	+.163 ± .088	−.145 ± .062	−1.601 ± .591
FSS–FS	−.025 ± .037	−.000 ± .026	+ .051 ± .331
FSH–FS	+.098 ± .048	+.004 ± .034	− .151 ± .419
FSD–FS	−.004 ± .050	−.004 ± .035	− .044 ± .442
FSC–FS	+.084 ± .043	−.037 ± .030	− .618 ± .374
FSHH–FSH	−.033 ± .039	−.018 ± .027	− .158 ± .325
FSDD–FSD	+.238 ± .039	+.011 ± .028	− .338 ± .393
GG–G	+.052 ± .122	−.069 ± .086	− .349 ± .398
GGH–GG	+.057 ± .097	+.095 ± .068	+ .478 ± .402
GGH_2–GG	−.297 ± .096	−.185 ± .068	− .750 ± .405
GGD–GG	−.057 ± .098	−.076 ± .069	− .374 ± .407
GGD_2–GG	−.154 ± .099	−.240 ± .070	−1.215 ± .414
GGHH–GGH	−.882 ± .089	−.228 ± .063	− .576 ± .375
GGDD–GGD	+.542 ± .095	−.087 ± .067	−1.145 ± .453
LL–L	−.143 ± .071	−.168 ± .054	− .902 ± .336

tive differences is +.163 units; of the negative differences —.188 units; of the entire series of 28 comparisons

—.012 units. Considering the differences individually in comparison with their probable errors[2] we note that if we regard a difference at least 2.50 times its probable error as statistically significant, 10 of the differences may

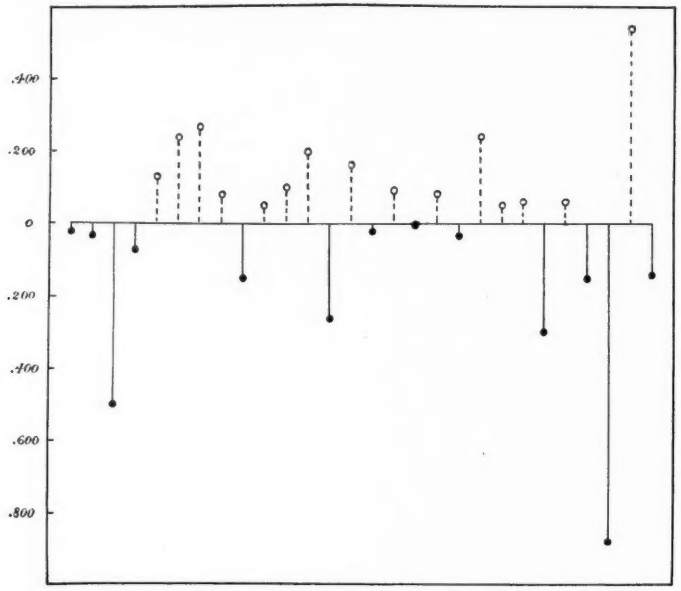

DIAGRAM I
Differences in Means.

be looked upon as trustworthy. Of these 5 are positive and 5 are negative. If we require $Diff./E_{diff.} = 4.00$, we find only 7 trustworthy cases, 4 positive and 3 negative in sign.

Diagram I shows graphically the amount and the sign

[2] It is somewhat difficult to decide just what ratio of the difference to its probable error should be used to indicate trustworthiness. As already emphasized, we have in reality two instead of one random sampling to take into consideration in the comparisons which we are drawing. The ratios $Diff./E_{diff.}$ are available to the reader who may assign to them any significance he sees fit. The general trend of the series furnishes much stronger evidence for a selective mortality than does the apparent statistical trustworthiness of any individual comparison.

of the differences between the general and the viable samples. Here the different comparisons are shown from left to right in the order in which they are given from top to bottom in Table V. The distances of the solid dots below the zero bar indicate the amount of the negative deviations, the circles above the positive deviations.

From all of these considerations, we conclude that seeds which produce fertile plants are on the average neither lighter nor heavier than random samples of the population.

While the results for the means furnish no evidence for a selective mortality, the standard deviations are very suggestive of its existence. In 19 cases, the S.D. of the seeds which produce fertile plants is lower than that of the series from which they were drawn, while in 9 cases it is larger. The deviation from the equality to be expected if the differences were due purely to an infinite number of random sampling is therefore

$$5 \pm .67449 \sqrt{.5 \times .5 \times 28} = 5 \pm 1.79,$$

which is perhaps statistically significant. The chances against the result being due to the errors of sampling are roughly the same as those against 19 heads and 9 tails, or *vice versa*, in coin tossing.

Not only the inequality of the divisions of the signs into positive and negative, but the magnitude of the deviations themselves evidence for a selective mortality which reduces variability without sensibly affecting the average. The 9 positive deviations average +.037; the 19 negative —.122; the whole 28, —.071. The far greater magnitude of the negative deviations is made clear by the generally greater lengths of the bars below the zero line in diagram 2. Considering the individual differences in their relation to their probable errors, we note that in 7 cases the difference is over 2.5 times its probable error. *All of these are negative in sign.*

The coefficient of variation, that is, $100\sigma/m$, should show most clearly whether both larger and smaller seeds fail

to develop, thus bringing about a reduction in variability which is independent of any change in the mean. The results given in the final column of the comparison table V, evidence even more strongly than the standard deviations in favor of such a selective elimination. They are

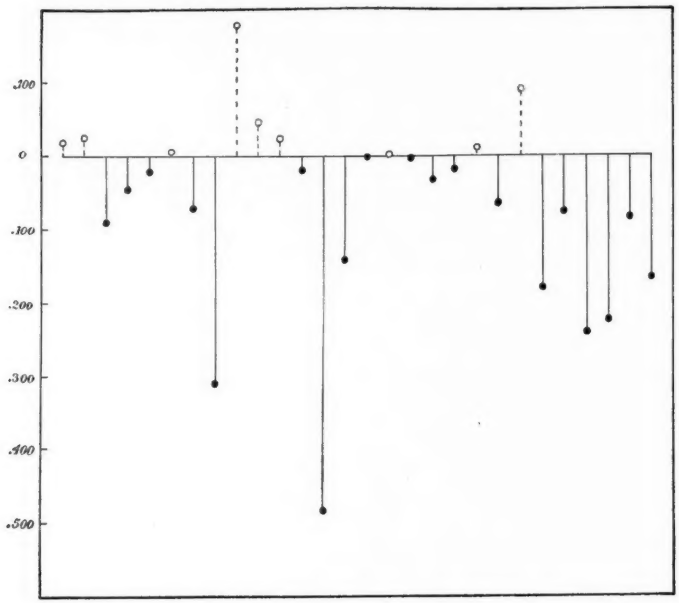

DIAGRAM II
Differences in Standard Deviations.

lower for the seeds which develop into mature plants in 21 out of the 28 cases. This is a deviation from equality of

$$7 \pm .67449 \sqrt{.5 \times .5 \times 28} = 7 \pm 1.79.$$

The averages are:

For positive deviations, $+.325$
For negative deviations, $-.712$
For all deviations, $-.453$

Diagram 3 makes the reason for these differences clear to the eye. With regard to their probable errors, the six

cases which are perhaps statistically significant, are all negative in sign.

Summary and Discussion

Taken altogether the data seem to me to indicate a real differential mortality in seeds of *Phaseolus vulgaris* in

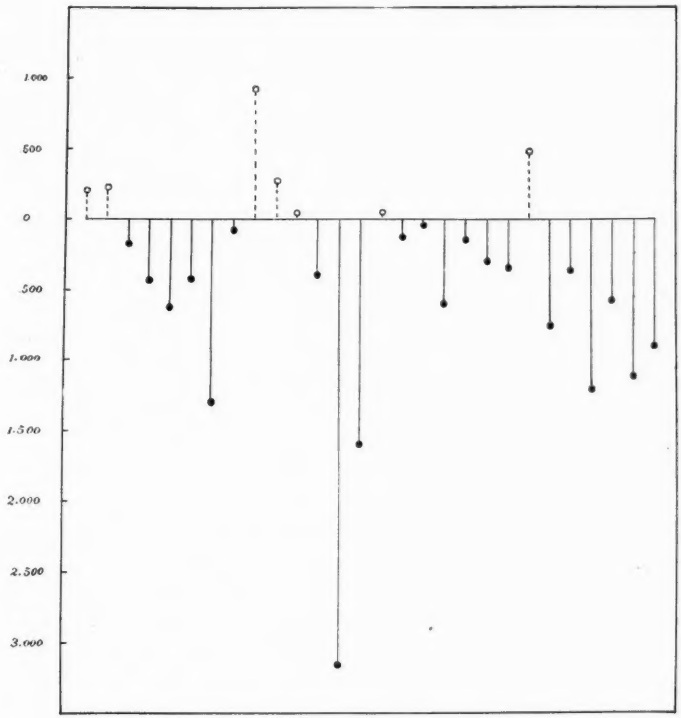

Diagram III
Differences in Coefficients of Variation.

field cultures. This selective death rate is of such a nature that the mean of the viable seeds remains practically the same as that of the original populations while their variability is reduced. In short, both large and small seeds are less capable of developing into fertile

plants than are those which do not deviate so widely above or below the type.

While the evidences in support of these conclusions are fairly strong, it must not be forgotten that we are dealing with a problem of great delicacy upon materials grown under conditions such that the accidental (purely non-selective) death rate must be quite high, and with records not especially collected for our present purpose. Positiveness of assertion must therefore be reserved until more critical evidence collected *ad hoc* is available. The reader will note, however, that the conclusions here recorded are based on many thousands of observations. Although experiments are already under way, the gathering of the data necessary for a more thorough investigation of the problem will be a long task, and it seems only right that the results obtained incidentally should be placed on record for the benefit of those who may have opportunities for like observations.

To me personally, the results were surprising. First, I had doubted whether a selective mortality could be detected by the methods used. Second, I had supposed that if a differential viability were found, it would be limited to a weeding out of the lighter seeds. This latter presupposition was based on the fact that a positive correlation had already been demonstrated[3] between the weight of the seed planted and the number of pods produced, and *a priori* it seemed reasonable to suppose that viability and capacity for forming plants with large numbers of pods would bear the same relationship to the weight of the seed. Both questions deserve much more detailed and refined study.

Two questions concerning these results will be foremost in the mind of the biologist: (*a*) What is the significance of the selective elimination for evolution? (*b*) What are the underlying causes of the differential mortality?

[3] Harris, J. Arthur, "On the Relationship between the Weight of the Seed Planted and the Characteristics of the Plant Produced," *Biometrika*, Vol. 9, No. 1, 1912.

The answer to (*a*) depends, as has been pointed out above, upon the inheritance or non-inheritance of the variations in seed weight. This question can not be discussed as yet, but from the data in hand, it seems to me likely that this selective elimination has little or no evolutionary significance. Certainly it is, as far as our evidence goes, not a cause of progressive change but only a factor tending to preserve an established type. It would then be an illustration of the "periodic selection" of Pearson.

The answer to (*b*) must be sought in the physiological, and of course ultimately, in the chemical and physical properties of the seeds of different weights. Experiments directed to its solution are under way.

COLD SPRING HARBOR, L. I.,
July 15, 1902

A CASE OF POLYMORPLISM IN ASPLANCHNA, SIMULATING MUTATION. II

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I may next state some further observations which I was able to verify again and again in regard to the transition of one form of the species to another. As I have said, forms intermediate between the saccate and the humped, between the humped and the campanulate, and even between the saccate and the campanulate, occur. This statement applies to external body form, and to some extent to the nephridia and other internal organs, with the exception, however, so far as I have yet observed, of the size of the contractile bladder. This latter seems to have its large size only in the small saccate type, and I have observed no indications of gradual transitions to the form possessed by the larger rotifers. More significant, however, is the case of the trophi. I have examined these in a great many individuals that in body form were more or less intermediate between the different types; but in nearly every instance the variations of this organ seem to be abrupt and discontinuous; the trophi are either of one type or the other. The only instances found that in any sense transgress this statement were the trophi of a few saccates produced as the result of the slow degeneration of the larger form, in the culture which I have before mentioned. These animals showed trophi that had plainly lost a number of the more delicate characters which I had otherwise found universal through such a wide range of material, and, simultaneously with this, they had become in a degree transitional between the two types; the angle of the inner tooth and a slight crossing of the tips plainly related them to the cannibalistic type, while in size and general form they

belonged to the other. I will record here also two instances in which I have found the cannibalistic trophi in the humped rotifer. The two specimens were almost the last humped individuals found in a culture on the verge of extinction through cannibalism; they were probably the progeny of campanulates. Both were large specimens of the humped type, one showing a rather heavy corona and rather small humps, and being, therefore, in some sense, of a transitional character. It bore campanulate trophi 257μ long—rather undersized—in which, however, the large lamellate teeth of this type were even unusually developed. The other bore typical campanulate trophi 270μ long, These animals contained large unborn humped rotifers of normal type, with normal trophi of 154μ and 170μ, respectively. In these two instances, therefore, the transition from the campanulate to the smaller type occurred one generation sooner in general body form than it did with the trophi, thus emphasizing the partial separateness and non-correlation between the variations in these differently formed structures.

Next as to duration of transition periods and the number of transitional individuals. If conditions are favorable the periods are very brief and the number of transitional types so few that they are readily overlooked unless careful search is made at just the right time. The entire population of a teeming *Asplanchna* pond readily changes from the saccate to the humped type in one week. As before said, the saccates give birth directly to forms with well-developed humps, and these humped young may be at birth as large or even larger than the parent type. One more generation of growth and reproduction may then give large-sized, fully typical humped individuals. Along with these abrupt transitions there usually occur, however, a lesser number that are a little more gradual. Individuals occur like saccates in all respects save that they possess the inconspicuous dorsal hump; others are small with the lateral and ventral (posterior) humps

scarcely showing at birth, but developing to a moderate extent rapidly afterward.

With less favorable conditions the transition is prolonged and the number of intermediate individuals is greatly increased. I have observed no instance, however, in which the species remained for longer than two weeks in a chaotic condition. Either the transition is soon effected or the numbers rapidly decrease and the species disappears.

Nearly similar statements may be made with regard to the transition from the humped to the campanulate type. As already stated, its advent usually occurs by the appearance of a very few individuals with the utmost abruptness. Aside from the fact that the ontogeny is here somewhat more extended—they, the young, being considerably smaller than the adults, with much less expanded corona—there is apparently little, if any, sense of transition. I think it probable that the humped individuals which actually give rise to the very first campanulates are individuals of somewhat extra size and vigor. Such individuals have been found at different times as well as in the case of the two mentioned in my first investigation, but their actual production of the young cannibals has not been observed. In any case their deviation from the ordinary humped type is not great and the usual transition has all the abruptness that the most pronounced mutationist could anticipate. Moreover, as long as the species is thriving and reproduction copious, the two forms remain separated from each other as sharply as do the most distinct species. This is the most frequent condition by far in which one finds them.

When, however, conditions become less favorable, which fact usually means that the food supply of the humped form is failing, a change intervenes. The humped individuals usually remain quite as they were, without reduction in size or loss of other characteristics, save a much slower rate of reproduction. But this reduces numbers, and especially the number of young.

The cannibals can and do ingest their full-sized congeners, but they are by no means successful in every attack. One may observe them, with empty stomachs, making scores of furious but futile attempts at capturing their adult neighbors. It is largely the young humpbearers which, though nearly full grown, fall ready victims to the all-embracing coronæ of the cannibals. Thus it follows that any reduction of the food supply of the lesser type immediately impoverishes the larger one as well. The consequences of this are curiously dissimilar in different cases, although always one of two results intervenes. The cannibals may become even more cannibalistic, destroying the entire humped population of all ages, and their own young as well, until the culture is finally obliterated by the death, from old age, of a few veterans which are without further food supply. This has happened again and again in my large culture dishes.[7] In a few cases it has happened that a culture, when at the point of extinction, would again revive by the multiplication of the humped form. This is due to the fact that the last starving cannibals, reproducing, as they always do, both their own type and the humped type as well, fail to eat up perhaps a single member of their humped progeny, which then survives to start a new cycle under less strenuous surroundings. I have carefully followed this decline and survival as thus stated.

In about half of the cases, however, a very different effect is registered upon the campanulate form by the lessening food supply and the falling numbers of the other type. It undergoes a considerable degeneration, which may perhaps reduce it to the form from which it arose, although I have not been able to fully demonstrate this. But forms more or less intermediate are produced by the starving cannibals. The trophi remain typical, but the enormous coronas, as well as the breadth of the entire animal, are much reduced. In the single instance already mentioned in which degeneration gradually reduced the humped type to a small size, and finally to the

[7] I have recently observed one very similar instance in nature.

most diminutive saccate form, I was surprised to find that the campanulates present in the culture degenerated, pari passu, with the other type. They became much smaller, lost their flaring coronas, and nearly every sign of their outward specialization. Yet, generation after generation, they maintained their cannibalistic habits, their heavy musculature, and above all the campanulate type of trophi, the only change in these latter organs being a reduction in size.

In the main, then, transitional periods are brief; transitional forms few. Unfavorable conditions prolong somewhat the existence of both. But the species always is soon eliminated or sets up a new equilibrium under the new conditions.

A few words further may be added at this point upon the matter of fluctuating variation shown by the different forms of this species. Without recording such variations mathematically, I have endeavored to ascertain as fully as possible the answers to three questions: First, how great is the amount of such variation? Second, is fluctuating variation especially correlated with one or other of the types of heterogenesis above described? And third, what causes are operative in producing it?

As to the amount of fluctuating variation, certain facts have already been mentioned that come under this heading. I will but add here the general statement that each of the three types is, in itself, highly variable—quite sufficiently so to be regarded as a decidedly variable species were it really an independent form.

As to the second point, the question of the correlation between fluctuating variation and the mutation-like transitions, this has also been partially discussed under the heading of transitional types. But it is necessary to add the unqualified statement that no evidence has been discovered for such correlation. Variation is one thing; heterogenesis another. The two phenomena contrast, rather than are related. Thus the transition from the saccate to the humped rotifer is often made when the

saccate type is in its most typical condition, at least so far as form is concerned. Of all the minor fluctuating forms found among the saccates the one that most suggests the humped type is that which I have characterized above as urn-shaped. The bulging sides of such a form might readily be thought to be the forerunners of at least the lateral humps; but during the entire study I have been unable to observe the humped form originating from this urn-like variety.

Furthermore, the saltations from type to type do not necessarily occur, and I think do not usually occur, when the amount of fluctuating variability is greatest. This is especially true of the formation of the campanulates from the hump-bearers. This transition occurs when the latter are at a culmination of development and vigor, and in this condition the species is, until saltation occurs, relatively uniform.

Under the third question, as to causes of fluctuating variability, I will record at present but two points, one general and one special.

The greatest amount of general fluctuation seems always to occur under relatively unfavorable conditions. Favorable conditions, on the other hand, tend to produce full development with relative uniformity among the individuals of any given type.

One special instance of variation interested me so much that I followed it whenever found, in the effort to get at its exact cause. This is the variation in the length of the three conspicuous humps which characterize the commoner form. The amount of this variation is, although I have not measured it, very great. The humps may be but angular projections upon the body's outline, or they may elongate until they might be appropriately described as finger-shaped. The type represented in the illustration, Fig. 1, may be taken as typical. This type is repeated in countless numbers, with but moderate variation, so long as conditions are normal, which means chiefly, so long as the food supply is uniform and ade-

FIG. 1.

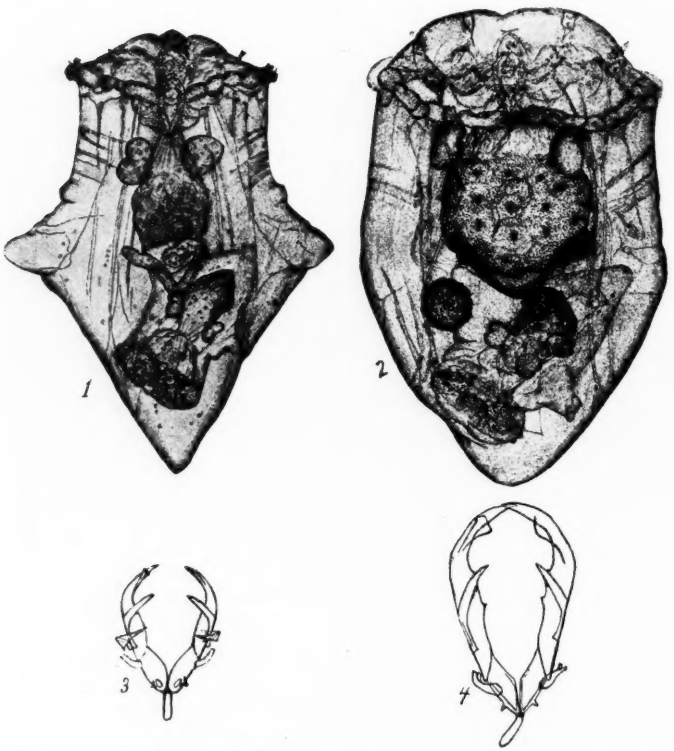

FIG. 1. *Asplanchna amphora*, OF THE HUMPED FORM (FORM *B*). SHOWING TYPICAL YOUNG DEVELOPING PARTHENOGENETICALLY WITHIN THE BODY OF THE PARENT. Magnification about 8 diameters.

FIG. 2. *Asplanchna amphora*, campanulate form (form *C*), showing heterotypic young developing parthenogenetically within the body of the parent. This figure is drawn from a specimen chosen because it exhibited well the heterotypic reproduction. In other respects it does not represent the true form of the campanulate type, the shrinking action of the killing fluid having both shortened and contracted the corona, obliterating thus the bell-like form and rendering the anterior portion highly convex instead of concave as in life. The convex end of Fig. 1 is, on the contrary, quite correct, the smaller type being much more easily killed in perfect form. Magnification about 8 diameters.

FIGS. 3 AND 4. Trophi of humped and campanulate forms, respectively. The contrast in size is inadequately shown by these figures. Had average specimens been chosen, Fig. 4 would have been twice the length of Fig. 3. In both figures the "accessory jaws" are omitted, they being so weakly developed as to be quite destroyed in the process of extraction. In Fig. 4 the upper lateral pieces, the outriggers, are omitted for the same reason. Magnification about 210 diameters.

quate. The individuals with smaller humps are always transitional or degenerative in origin.

But what could be the cause of the hypertrophy of the humps to fully double their usual prominence, and this in individuals that always gave evidence of starvation? Such individuals occurred in certain cultures in considerable numbers, and constituted a very extreme type; the animals were always much more transparent than any others, the body wall being thin and the internal organs usually pale, shrunken, and undeveloped, the stomach empty, and embryos lacking. The general body form was extremely slender, with corona but two thirds average width, while the ventral, or rather posterior, hump was not only long, but developed a secondary prolongation, as it were, from the end of the original one. Such animals swim, all but habitually, with the lateral humps retracted, and in this condition are so slender as hardly to suggest the genus *Asplanchna,* the form being apparently more nearly that of *Hydatina.* But with the thrusting out of the lateral humps a singular transformation occurs; these structures are so long that their expanse equals or exceeds the animal's length, and so slender that the animal's forward motion bends them backward. In my notes I designated these extreme animals as the "cross-bow type."

As already mentioned, they occurred in considerable numbers in several of my mass cultures. I also obtained them several times under controlled conditions in isolation experiments, but I found no clew to the cause of their production until I discovered that they were frequently produced by the gaint campanulates, and especially by the campanulates that were *Moina*-feeders. It seemed very striking that this variant, which carried the development of the humped form to its utmost extreme, should be thus produced by the robust companulates in which there are no humps, and in which, indeed, all the characteristics are at the farthest possible remove from the type in question. Yet these cross-bow hump-bearers

formed a regular part of the progeny of the massive crustacean-feeders. All but invisible, they swam restlessly about seeking for available food, which was not present, until many of them fell victims to the greedy members of the parental stock.

This combination of overfed parent and foodless progeny offered the suggestion of the cause I was seeking, which was then readily confirmed by experiment. Maximum nutritive conditions before birth and the entire absence of available food for at least 24 hours after birth produces the slender transparent type with the hypertrophied humps. Under these conditions the body wall, and its projections, which are highly developed even at birth, continue to develop for a considerable time afterwards, undoubtedly withdrawing nutrition from the internal organs—stomach, digestive glands, ovary, etc.—these thereby undergoing a partial atrophy.

A certain interest attaches to this explanation, because it not only furnishes the rationale of an extreme type of fluctuating variation in this rotifer, but because the facts closely parallel the incidents in the development of the male of the same species. The males at birth lack, of course, the chief internal organs of the female, and can not draw upon them as sources of nutrition, but they do draw upon the rudimentary digestive tract until, before death, it has frequently quite disappeared. Moreover, the males undergo a progressive development of the body wall and to some extent of the humps during the two to four days of their active life. The male thus becomes more differentiated in the active portion of its organization, absorbing meanwhile what little inactive tissue there is to absorb. The same thing happens to the young foodless female, save that there is more tissue to absorb, and the process is not carried so far.

Sufficient investigation would doubtless unravel each of the other minor fluctuations which the three forms of the species undergo, and most of them will all but certainly resolve themselves into factors of nutrition. Few

species of animals are capable of so numerous and varied nutritive transitions and respond to them in so fundamental and varied manners as does this *Asplanchna*.

Before closing this paper it becomes a disagreeable necessity to attempt some more definite systematic placement of the forms of *Asplanchna* here discussed. The task is a difficult one for several reasons. In the first place, it is obvious that the facts here recorded tend to disturb our very conception of what constitutes a species in this genus. If we accept the interpretation of polymorphism as, on the whole, a little more applicable to the facts of heterogenesis here cited than would be the interpretation of mutation, the question is obviously raised whether several of the other *Asplanchna* types hitherto described as distinct species may not likewise be closely related genetic forms, connected, as are those here described, either with each other or possibly with these very types. Thus a relationship is readily thinkable between *A. ebbesbornii* and *A. intermedia* or *A. sieboldi*, or possibly of one or the other with *A. brightwelli;* although the disparity of the males in this last type renders relationship less probable.

Moreover, in the literature of the subject the claim has been made at least once that such a relationship exists between European forms, as the following quotations from Wesenberg-Lund[8] in which he cites Daday to this effect, will show:

> Uber die Fortpflanzungsverhältnisse der Asplanchnen kann ich Folgendes mittheilen.—v. Daday ("Ein Fall von Heterogenesis bei den Räderthieren." *Mathem. und Naturw. Berichte aus Ungarn*, 7. Bd., 1888–1889, p. 140) hat für *Asplanchna sieboldi* einige ganz merkwürdige und bisher exceptionelle Fortpflanzungsverhältnisse geschildert. Seiner Meinung nach findet man hier zwei verschieden geformte Weibchen, theils solche, die den gewöhnlichen schlauchförmigen *Asplanchna*-Typus haben, theils solche, die den eigenthümlich geformten Männchen dieser Art gleichen; diese sind durch 4 conische Erhöhungen characterisiert, und sind diese Erhöhungen derartig vertheilt, "dass je eine auf die Mittellinie des Bauches und der Rückseite, eine auf die rechte und eine

[8] Wesenberg-Lund, C., "Ueber danische Rotiferen und über die Fortpflanzungsverhältnisse der Rotiferen," *Zool. Anz.*, 1898, Bd. 21, pp. 200–211.

auf die linke Seite fällt, wodurch, von vorn betrachtet, die Form eines gleichschenkeligen Kreuzes sichtbar wird" (Daday, p. 153). Jedes dieser zwei verschieden gebauten Weibchen vermag sowohl Weibchen ihrer eigenen Gestalt parthenogenetisch hervorzubringen, als auch Weibchen der anderen Art; ferner auch Männchen und, nach der mit diesen erfolgten Begattung Dauereier (pp. 206–207).

Daday's work on the rotifers has in general been frequently criticized and all but discredited, and this observation on his part of a reciprocal relationship between *A. sieboldi* and a saccate *Asplanchna* fares no better at the hand of Wesenberg-Lund. He replies that he has himself reared *A. sieboldi* in an aquarium for a month, that he has studied them thoroughly and has found no such reproductive phenomena. He continues, that Daday has simply been mistaken in his observations, having failed to distinguish the humped *A. sieboldi* from the saccate rotifer, because the humps of the former species are often retracted, giving it for the moment a saccate form.

This criticism of Daday's reported observations may of course be correct, but it seems as naïve as it is severe. It is of course true that the humped rotifers retract the lateral humps; but the position of these protuberances always remains marked by folds of the body wall, while the ventral hump is not retracted at all. Daday must indeed have been a poor observer to be thus deceived, the more so, in that the moment these animals are placed under the pressure of a cover glass or even in a very shallow drop of water on a slide, the pressure of the cover glass or their own weight forces them to expand the humps and instantly reveal their type of structure. In the light of my own study it seems far more probable that Daday was correct in his reported observations than that Wesenberg-Lund is correct in his criticism of them. The fact that Wesenberg-Lund reared the humped *Asplanchna* for a month without the occurrence of heterogenesis is of no especial significance. The writer has reared the humped form discussed in the present paper for longer periods than this with the same result.

Heterogenesis is confined to special periods or caused by special conditions as above set forth.

However, not only is the question of species confused by the presence of heterogenesis in the genus, but another difficulty which I had not anticipated manifests itself; viz., the discovery that the descriptive work which has already been done upon the genus has not, even the best of it, been sufficiently accurate to be trustworthy. I make this statement with the utmost reluctance, and only after I have spent weeks of effort to bring my observations upon single points into accord with the statements of Rousselet, who is not only the highest authority on the group in question, but who has, as already stated, made the last and most detailed pronouncement upon the species of the genus. I have failed, however, in my efforts. Nor are the discrepancies such as may, with probability, be explained by the assumption of differences in the material which we have examined. Thus, to take an example from Rousselet's description of the jaws. He says:

> At the tip there is really but a single point . . . ; on crushing the jaws a thin, chitinous ridge seen in side view is bent over and simulates a second tooth.

Hudson, in his supplement, has also spoken to similar effect, viz.:

> When the ramus is subjected to pressure from above the deep plate is bent by the glass (to which it stands at right angles), and its free lower corner is twisted, so as to look sometimes like a second tooth, just below the extreme apex, sometimes like a small plate.

Now in spite of these statements I seemed to see the thin lamellate plate-like second tooth near the apex of every jaw in case the conditions for its vision were at all adequate, and in the giant campanulate this structure, so delicate in the ordinary type, becomes greatly developed, forming a large cutting tooth, which, when the jaws are closed, meets with its fellow of the opposite side, in the middle line. That this thin triangular tooth in the ordinary form was a false appearance produced by the

bending over of the corner of a ridge by the pressure of a cover glass seemed improbable, and I immediately put it to test in various ways. For one, I extracted a large number of the trophi by means of potassic hydrate in deep watch-glasses. Here there was obviously no pressure, yet the structures in question were quite visible, even before the trophi had been transferred to a slide, or touched by any instrument. Moreover, these thin lamellate teeth are never quite symmetrical on the two rami, and this delicate discrepancy is always on the same side of the animal, as I ascertained later in stained and mounted preparations. I carried my study of the trophi farther by mounting many which I had extracted in deep hollow-ground slides, including with them a small bubble of air. By giving the slide a quick tilt the air bubble could be made to strike and overturn the trophi in different ways. By then replacing the slide quickly under the microscope, views could be had of the trophi before they had settled to the ordinary horizontal position. A half hour of such attempts readily furnished views of every part of the trophi, seen from almost every possible angle. Portions so thin as to be invisible in one view become visible in another; optical sections at all points make possible the arrival at the correct form. I regret that in my drawing I have been able to show so little of the delicate complexity of these structures; but Rousselet's view of their structure—that "the chitinous material is bent at right angles throughout the length of the rami, forming an inverted L in cross section"—is certainly very far from correct. The structure varies at different points; ridges thicken and fade out in complex and sinuous fashion, quite as we should find them in the complex chitinous jaw of an insect, or, for that matter, in the jaw-bone of a mammal.

The tips of the jaws are interesting, and I find no description of the jaws of any species of *Asplanchna*, by any author, which coincides with my observations. Nevertheless, this may be due to the inadequate study of

these difficult structures by systematists who can devote but little time to a given point. I find the two rami are never alike at the very tips. I am not speaking now of the delicate lamellate teeth already mentioned which are a little distance removed from the tips, but of the very extremities. Of these latter, one is bifid, or ends in two delicate tips; even these again are never quite symmetrical, but the one which is toward the animal or posterior is a little smaller and shorter. Furthermore, the split in the tip of this jaw is not a simple cleft such as one might produce by splitting the end of a stick with a knife, but is a triangular groove, the base or open side of which is toward the inside or concave aspect of the ramus, the apex toward the outside. As aforesaid, this cleft divides the tip of the ramus, but it is also continued on the inner aspect of it considerably farther than it extends on the outer, becoming thus shallower and shallower as it extends farther from the divided tip. The opposite ramus is not bifid, but tapers to a point, and the tapering is of such a nature that the jaw near the tip is more or less triangular in cross section, so as to fit, not only into the cleft between the tips of its fellow ramus, but farther into the triangular groove on its inner side as well. Thus these delicate chitinous jaws, when closed, lock together in double manner.

The study of hundreds of examples of the trophi of the humped rotifer as it occurred in the material first examined left upon the mind of the writer a very distinct impression of the minute delicacy of detail and very great uniformity which prevails in these structures. Variability seemed almost wholly confined to the matter of size.

Turning briefly to the trophi of the campanulate type, I will say that they differ regularly from those just described, not only in the features shown in the figure, such as general size, breadth of rami, more acute angle of the lower inner tooth, etc., but in other marked features besides. The inner tooth, smaller in proportion as well

as set at a different angle from the corresponding structure in the humped type, is here fused with the ramus instead of being merely bent over inward from its outer margin. But the tips differ most; the secondary lamellate teeth, as before mentioned, become very large, though variable, structures. They always meet in the middle line when the jaws are closed; they have wavy or corrugated surfaces, and thin down to a sharp cutting edge. The tips of the rami are modified most of all. They are slender and greatly extended in length, meeting and passing at an acute angle. Neither tip is bifid, and the asymmetry between the two rami is much less marked. The jaws do not interlock, when closed, in the sense in which they do in the humped type; instead, the tips invariably cross, like the mandibles of a crossbill, the farther closing being prevented by the meeting in the middle of the lamellate teeth. Occasionally I have noticed a campanulate whose jaws had sheared past in the wrong way; the lamellate teeth then did not meet to prevent farther closing, and the animal had apparently lost control of the organs, as the two halves remained crossed well down to near their bases.

Returning to Rousselet's description of the trophi of *A. amphora*, which must, of course, be compared only to the trophi of the humped type, I will say that despite the discrepancies in detail which I deem due to inaccuracy of observation, it remains true, nevertheless, that his general figure of the trophi of this species coincides essentially with the general appearance of the trophi as I find them in the humped and saccate types, and this constitutes a fair reason for assigning, provisionally, the material which I have studied to the species *Asplanchna amphora*.

However, I can not leave this matter of the trophi without instancing a surprising observation which I have made the past summer on the trophi of the related species, *Asplanchna brightwelli*—an observation which again complicates, in an entirely new way, the question of species in the genus *Asplanchna*.

As soon as I had discovered the fact that the humped *Asplanchna* which I was studying was represented by a saccate type which in many characters approached closely to *Asplanchna brightwelli,* I began an extended search for this latter species, in order to study closely the question of relationship or non-relationship. At different times, throughout a period of one year, I succeeded in finding *A. brightwelli* in five different ponds in my own vicinity. The species tenants ponds of a different character from those in which the larger *Asplanchna* flourishes, and is associated with a somewhat different micro-fauna. In but one instance have I found the two species developing together, and in this case the larger *Asplanchna* did not pass beyond the saccate condition, in which it was also present but sparingly. The resemblance of its occasional representatives to the more numerous and likewise saccate individuals of *A. brightwelli* was so great as to almost prevent its detection. Only my constant work with the larger species could have sharpened my attention to the point of noticing any especial lack of homogeneity in the material. Yet the saccates of the larger species were regularly a little longer and about one fourth broader than the adult *A. brightwelli.* They differed also in a number of minor constant characters. But none of these have hitherto found place in any specific descriptions, with the exception of the difference in the trophi. The trophi of the larger saccates agreed with the description and figure which I have given in everything save that they were a little undersized. The trophi of *A. brightwelli* agreed in their general outline with the figure given for this species by Rousselet; they possessed the more delicate, perfectly oval contour, and invariably lacked the large inner tooth, just as Rousselet asserts that he has always found them to do. Into the question of the form of their tips and the presence or absence of the all but invisible lamellate teeth I do not go. Such study as I have given them led me to think that they were constructed in these respects

essentially, but not exactly, as were those of the type which I had already studied. I was much pleased to thus substantiate, at least in a general way, on this American material, Rousselet's judgment on the distinction between the trophi of these two species. I will add that a score of culture experiments started with single individuals of the two types fully confirmed their distinctness. Despite their very close resemblance, I reared from one set of the delicate saccates the humped *amphora* type with which I was so familiar; while parallel cultures, with identical conditions as to food and temperature, produced no modification in the *A. brightwelli* other than a slight increase in size.

I therefore reached the conclusion that, delicate as are the differences which separate the saccate form of *A. amphora* from the invariably saccate *A. brightwelli,* they were none the less sharply demarcated. Ignoring other features, it seemed perfectly safe to trust the one character of the absence or presence of the larger inner tooth on the trophi.

Imagine my surprise, then, when, upon visiting an entirely different locality—Custer County, South Dakota —I discovered an *Asplanchna* in countless numbers which completely upset this distinction and introduced me to a seemingly new type of variation within the genus.

It was in the charming little mountain lake (or rather reservoir, for the original site contained a mere pool which has now been increased to a depth of 80 feet by an artificial dam) called Sylvan Lake, that I came upon the rotifer in question. The lake was indeed swarming with rotifers of different species, which constituted the majority of its plankton. Monarch of them all, and profiting greatly by its superior size and ingesting power, was a superb *Asplanchna.* Aside from a slight excess in size every outward character indicated *A. brightwelli.* Moreover, I had found the species in the very nick of time, for both males and resting eggs were copiously present. Among very large numbers of these which I

immediately examined not one differed outwardly from the *brightwelli* type. But examination of the trophi yielded the astonishing result that in every instance they bore a strong inner tooth in the exact position in which this is found in *A. amphora*. I examined large numbers of them and found that in all the features which I could study with the facilities I had in the field, there was no obvious variation whatever. It should be mentioned that in outline these trophi presented the close approach to a perfect oval which is characteristic of the *brightwelli* type. The strong inner tooth alone gave them decidedly the aspect of the jaws of *Asplanchna amphora*.

This discovery is plainly again confusing, as to specific distinctions between the types. Fortunately, however, it serves at least to clear up certain contradictions in the literature of the subject. Rousselet, in the article above mentioned, dealt especially with this point. He figures the jaws of *A. brightwelli*, to use his own expression, as he has "invariably found them"—*i. e.*, with an oval outline and without the inner teeth. He concludes that the earlier writers on the genus—Dalrymple, Brightwell, Hudson—had certainly confused two different species of *Asplanchna*, describing the trophi of *A. amphora* as belonging to *A. brightwelli*.

My examination of the Sylvan Lake material shows that no such error need be ascribed to them. *A. brightwelli* simply exists in two distinct races (genotypes?); Rousselet has invariably found but one of these, just as I myself have done in my own vicinity; while Brightwell very probably found and described the other, which I have found so abundant in the South Dakota lake.

The finding of *A. brightwelli* with two distinct types of trophi may seem but a trivial matter, but taken in its full connection it is not without interest. *A. brightwelli* seems, in general, an all but constant species. Yet, judging by morphological test, it should be closely related to *A. amphora*, a species which experiment shows to be phenomenally variable.

What, then, is the relationship—the physiological and genetic relationship—between these two types? Jennings in his recent work on the "Characteristics of the Diverse Races of *Paramecium*" has prophesied that the more exact study of the life history of rotifers will demonstrate that much of their apparent variability is really due to the presence, within specific limits, of numerous fixed races.

Now the study, as here outlined, of the variation of *A. amphora,* brings to light a condition which in no wise substantiates this prophecy. No fixed races are present; but strongly demarcated yet temporary types, on the one hand, and fluctuating variations, on the other, which are all or nearly all the result of nutritive stimuli. Is it possible that, in spite of this, the closely related *A. brightwelli* will present the fixed races which Jennings suggests?

I have aleady indicated that a series of about twenty culture experiments with the type of *A. brightwelli* first found by me yielded no significant modification. At the present writing I am again following this species in copious natural development and again conducting a few mass cultures without finding anything but farther proofs of constancy.

I am also succeeding in rearing very large numbers of *A. brightwelli* of the type whose trophi present the inner tooth. The resting eggs, which were brought from Sylvan Lake the preceding August, were kept over winter in a small amount of the lake water and hatched out in March by adding tap water and raising the temperature by placing the dish in the sunlight. The culture medium has slowly been quite changed to the somewhat alkaline and saline water of the writer's locality. The cultures have also been heavily fed upon organisms to which they are certainly unaccustomed in nature. Some cannibalism has been induced. But the trophi remain obstinately true to their own type, and the general morphological changes have been confined to a considerable increase in

size of a few individuals, with perhaps a somewhat disproportionate expansion in breadth of corona. Yet the results of a preliminary six weeks' culture of this type of *A. brightwelli* are essentially similar to those which followed my attempts to modify the first type: they are negative.

Much more extended and varied experiments must be made before reaching final conclusions upon the constancy of these two races of *A. brightwelli.* Yet they certainly promise to bear out in the main Jennings's prediction of relatively fixed races within the species.

Yet the foregoing does not entirely complete the picture of variation as I have found it in *A. brightwelli.* While the rearing of thousands of individuals and the examination of a very large amount of material in nature give the appearance of two stable genetic types, yet in the rarest instances mutation-like changes of the most marked character probably do occur, just as they do in *A. amphora.*

While at Sylvan Lake it occurred to me that the very favorable conditions under which *A. brightwelli* was there developing, including the preying upon a number of different organisms, were as well adapted as possible to bring about mutational changes such as I had found to occur in *A. amphora.* Day after day I examined large amounts of material with wholly negative results. But a favorable morning at the very close of my stay at the lake enabled me to collect several liters of plankton as thick as cream in consistency, with perhaps four fifths of its bulk living *Asplanchna.* Pouring this in the thinnest possible layers, into broad dishes, and placing these above a black surface, I proceeded, by means of a powerful reading lens, to search for any individual *Asplanchna* showing marked deviation from type. Minor deviation could not, of course, be thus detected. To my great surprise, my search was finally rewarded by the finding of three individual rotifers, and three only, of quite astonishing proportions. They were certainly *Asplanchna;*

that they were derived from the *brightwelli* I of course have no proof, but in the light of my study of *A. amphora* it seems probable. They were campanulate forms, differing from the slender saccate *A. brightwelli* even more than the campanulate *A. amphora* differs from the smaller types of its species. Seen in dorsal view, when freely swimming in a drop of water without cover glass, they presented almost the form of an equilateral triangle with one rounded corner; this was the posterior end; the entire opposite side being taken up by the loose flapping corona. I regret that, in my haste, I was unable to study these forms precisely, and much less to prove their relationship. But I hope that the isolated observation may perhaps induce others to seek among crowded stocks of *Asplanchna* of different species for rare and much modified forms. If, as I believe will be the case, they are found to occur occasionally in *A. brightwelli* and perhaps other species, it will throw an added light upon the changes which so readily take place in *A. amphora*. The rarity of their occurrence will render clearer the relationship of the phenomena to the recognized instances of mutation.

Before closing the discussion of facts relative to the specific determination, statements must be made with regard to the males and to the resting eggs. Similar males are produced by all three of the forms which the amphora-like *Asplanchna* assumes. The humped and campanulate types produce them copiously; the saccate type but rarely and at periods when it is about to pass over into the humped form. These males are always of the well-known type bearing two lateral humps. They quite agree with Rousselet's determination, except that he evidently assumes the size to be uniform, whereas I find it to be extremely variable, the limits being as three to one. The largest males, often present in abundance, reach fully the size of the humped females; *i. e.*, a length of 1500μ. The cause for the wide divergence in size is the varying degree of development at birth. This affects them as it affects the young females, except that the young males,

being unable to feed and thus continue their development, are obliged to remain at approximately the same divergent sizes at which they are born.

In regard to the resting eggs, they are, of course, as are the males, produced by all three types, and but rarely by the smaller saccate form. The number produced by one individual varies greatly with the degree of nutrition. But one to three are matured if the females are poorly fed after fertilization; whereas as many as six are frequently present at one time in the body when nutrition is high, and very rarely as many as nine may be seen. The large campanulates usually show a high number, but it does not exceed the maximum produced by the humped form. The color of the egg, which Rousselet uses as a specific character, is variable in this species. In individuals fed on *Paramecia* the eggs are quite white; in individuals reared on *Brachionus* they are light yellow to orange; while in *Moina*-feeders they are dirty white to brown. Again, the volume of yolk, *i. e.*, the filling or not filling of the egg cavity, which Rousselet also regards as important, I find to be highly variable in the eggs of both this species and of *A. brightwelli.* It is partially a matter of the age of the egg; but eggs are frequently deposited in the most different conditions with regard to this character. There remains the size of the egg and the appearance of the egg coats, both of which are highly characteristic and relatively uniform. The size of the egg is much less, relative to the size of the animal, than is the case in *A. brightwelli;* but the actual size is larger and exceeds the dimensions given by Rousselet for *A. amphora,* viz., from about 200μ to 225μ, as contrasted with his figure, 170μ. This is surprising, in that, in the case of *A. brightwelli,* my measurements of the resting egg—170μ to 190μ—is less than the figure—205μ—given by Rousselet.

The egg envelopes, which I have studied in an almost indefinite amount of material, grown under very diverse conditions, are the most uniform and at the same time the

most peculiar feature which I have found in the species. They plainly do not agree with Rousselet's characterization of the egg of *A. amphora:* "The outer shell envelope consists of numerous much smaller globular transparent cells" (smaller than the cells in egg coat of *A. brightwelli*) "through which a finely dotted inner membrane can be seen." I find that at a certain intermediate stage of development a dotted inner membrane can be seen, the dots being the ends of either tubes or rods making up a thick inner coat; the rapidly developing outer shell, however, soon obscures these dots and the coat assumes at first a wrinkled, then a heavily corrugated, surface. The corrugations are so disposed that many of them converge at two opposite poles of the egg. I deem it quite impossible that this characteristic and beautiful structure should have been overlooked by any one studying this species in detail and with the full characters which it possesses in the writer's vicinity. It therefore seems very probable that the type of *A. amphora* studied by Rousselet was not identical with that studied by the writer, and it may accordingly prove necessary to eventually separate the form I have studied from the original type of the species, ascribing it varietal rank, based on at least this one character of the egg coats. The systematic predicament in which this would place these beautiful rotifers would indeed be pathetic or intolerable or humorous, according to our attitude toward things systematic. We should have two varieties, separated from each other by a single fixed character only, and one of these varieties would comprise within itself, besides a host of minor variations, three distinct types, each of which differs from its fellow, not only more than do the varieties differ from each other, but more than the whole species, at its nearest point of approach, differs from its closest congeners.

There is not the least known reason why actual facts of genetic relationship should not be as complicated as this, and if they are so we must deal with them systemat-

ically in some fashion. It is evident, however, that the species in question and other allied forms should be more intensively studied by workers in other localities before we venture upon the final solution of so intricate a question. For the present all that needs be said is that the material studied by the writer and designated by the phrases, the *saccate*, the *humped*, and the *campanulate forms*, belongs to the species *Asplanchna amphora*, as at present constituted; and it seems no less certain that this material is sharply segregated from *A. brightwelli*, despite the exceeding closeness of this latter species to the above mentioned saccate form of *A. amphora*.

A brief résumé of the chief characters of *Asplanchna amphora*, as here studied, will be of use to rapid workers. It is as follows:

Species trimorphic, each of the three forms showing fluctuating variation and occasionally intergradations.

Form *A*, saccate type, produced from resting egg and multiplying by rapid parthenogenesis, through several generations; corona about equaling diameter of body or less, nearly circular in outline, agreeing with the cylindrical body, which rests on side when water is withdrawn; body without humps or with small dorsal hump only; flame cells varying in number from approximately 20 to 40; contractile vesicle large; trophi as in next form, except smaller—about 95 μ to 135 μ long. Length of entire animal 500 μ to 1,200 μ.

Form *B*, humped type, characteristically known as *Asplanchna amphora*, originating from form *A* by rapid saltation and reproducing chiefly its own type; body conical, strongly flattened dorso-ventrally, with one posterior, one dorsal, and two lateral humps of varying size and habit of carriage; corona oval, agreeing with the flattened body, which causes animal to rest on dorsal or ventral surface when water is withdrawn; flame cells 40 to nearly 60; contractile vesicle small; trophi strong, typically from 150 μ to 170 μ in length, though varying from 130 μ to 200 μ, enclosing when closed an area which is not oval but widest in its distal third, with prominent tooth projecting inward seemingly from the inner though really folded over from the outer margin of each ramus, delicate lamellate teeth near the tips and the two rami interlocking when closed by means of one bifid and one pointed tip; accessory jaws, as also in forms *A* and *C*, very weakly developed. Length of entire animal approximately 1,000 μ to 1,800 μ.

Form *C*, campanulate type, originating usually from form *B* as a result of cannibalism, and reproducing both its own form and form *B*;

body very broadly saccate to broadly campanulate in form, with very heavy walls and musculature, strongly flattened dorso-ventrally, never with humps; corona oval and very broad, its breadth frequently equaling the length of the animal; anterior end of animal, within corona, concave instead of convex; flame cells approximately 80 μ to 115 μ; contractile vesicle small. Animal resting when water is withdrawn on dorsal or ventral surface; trophi very large, typically from 300 μ to 340 μ in length, enclosing a narrowly oval area; inner teeth relatively less prominent than in preceding types, set at an acute angle with the ramus and more firmly fused with it than in the preceding types; lamellate teeth near tips of rami much developed and meeting, with cutting edges, in middle line; tips of rami not interlocking but shearing past each other when closed. Length of entire animal approximately 1,800 μ to 2,500 μ.

In conclusion, it may be pointed out that the type of variation shown by the rotifer here discussed seems somewhat peculiar, in that it lies seemingly on the line between germinal variation and variation which is commonly supposed to be somatic. To use recent phraseology, it is difficult to say whether the types which this species of *Asplanchna* produces should be called genotypes or phenotypes.[10] They are like genotypes in that when once produced they manifest a marked tendency toward stability, each type reproducing itself through a number or even a multitude of generations after the special conditions which favored their origin have ceased to be present. They are to some extent like phenotypes in that this stability is less than that of true species, yielding, though rarely, to degenerating or other modifying conditions.

[10] As the proof of this article passes through my hands, one of the above terms—"phenotype"—is already a matter of ancient history; while "genotype"—used here obviously in the sense in which it has been used by Jennings—has gone down, so far as this meaning is concerned, before the onslaughts of a whole series of terms, of which "biotype" is perhaps the momentary victor. With malice aforethought, the writer allows the terminology to stand as written, for the reason that, however little others may concede the point, he believes it better to retard the fixing of terms—better to keep our concepts in these fields as fluid as possible, rather than to do the reverse. Facts—on the zoological side at least—are too few; new data will certainly damage prematurely fixed definitions. Some such facts—due to the study of other rotifers and protozoa—are already known to the writer which harmonize even less than the facts of the present paper with the rigid conceptions which some set forth with show of finality.

It is worth noting—though this is in part but restating the last thought in different language—that the variations here described differ from the majority of those recently recorded for minor invertebrates;[11] for example, the modifications in *Daphnia, Bosmina,* and *Asplanchna,* so carefully observed by Wesenberg-Lund. These latter variations are in the main variations in external form only, and seemed to be pure reactions to external conditions, taking place, for example, when the surrounding medium has reached a certain temperature, and again lapsing very soon after the temperature has dropped. Such variations fall naturally under the rubrics of seasonal polymorphism, temporal variation, or cyclomorphosis. The variations which we have studied in *Asplanchna* refuse to be thus classified.

It is true that the stability of these variants is markedly different, being greatest for the humped type and least for the minor saccate form, but a stability that tends strongly to resist external influences is none the less obvious for each. And this seems to the writer to render it highly probable that each of these variations is of germinal origin. If this is the case it is the more striking that this germinal variation is itself a variable and elastic quantity, originally initiated by nutritive causes.

In one sense only may it be said that these mutational variations do occur in a rhythmic or cyclical fashion, in that, namely, each form may produce a fertilized or resting egg that tends to return to the common starting point. The variations are therefore obviously not transmitted through the resting egg as they are through parthenogenetic ova. It is, however, by no means certain that there is complete community of kind in all the young hatched from resting eggs. Such observations as have already been made seem to show that the progeny of the resting eggs of this species are by no means uniform,

[11] Some of the variations recorded in the recent work of Woltereck approach more closely to those here recorded for *Asplanchna.*

physiologically or morphologically. Some stocks seem larger than others from the start, and apparently gave rise more readily to the second and third types. It will require much careful experiment to ascertain the cause of these diversities, and whether a tendency toward the transmission of variations actually lies in the resting egg.

If such proves to be the case, light will be immediately thrown upon the farther problem, namely, whether the saltations here described are intimately related to a true species-making process. All in all, it seems that they probably are thus related, especially as the forms produced parallel so closely other types of the genus which are now universally regarded as definite and circumscribed species.

But are these other types of the genus definite and circumscribed species, or are they (some of them at least) but semi-independent types, occasionally brought into existence by unusual nutritive conditions and then maintaining for a time only their partial or complete autonomy? Unfortunately these remaining forms of the genus are not accessible in the writer's vicinity. But they would seem well worthy of careful study, both observational and experimental, where they may be found, and it seems to the writer that such study, sufficiently prolonged, will bring to light a species-making process in rotifers which is somewhat different from any as yet demonstrated in the animal kingdom.

It is just possible that these saltational phenomena may be purely local, or at least greatly exaggerated in the genus *Asplanchna*. The food reactions of this genus are undoubtedly extreme, and the development of their parthenogenetic ova in close proximity to this spasmodic and very variable nutritive supply may possibly make this genus exceptional. But no fundamental organic phenomenon is wholly isolated and unlike the phenomena of other species. If nutrition can modify the germ cells in the genus *Asplanchna* and thus bring into existence new types, nutrition surely must be a factor on a wider scale.

SHORTER ARTICLES AND DISCUSSION

AN UNUSUAL SYMBIOTIC RELATION BETWEEN A WATER BUG AND A CRAYFISH

WRITERS on animal ecology and popular entomology have made us familiar with a remarkable habit of various species of water bugs belonging to the genera *Zaitha* and *Serphus*. In these forms it has been established that the female seizes a male and by superior strength and apparently against his will, covers his back with her eggs. These adhere together and to his tegmina to form a dense mass as thick as his own body. Converted thus into "an animated baby carriage" as Howard puts it, the male carries the whole brood about with him until they hatch, providing them with protection and, possibly, improved aeration. It is worthy of note that the habit has been observed in widely separated parts of the world, viz., both coasts of America, Europe, and Japan.

The writer has observed a somewhat analogous adaptation in another group of aquatic Hemiptera, the Corixidæ—a habit that appears to be so extraordinary that he has refrained from describing it until it should have been found to be other than a local instance. Quite by accident he discovered that a similar observation had been made previously by S. A. Forbes[1] so that it seems rather improbable that the circumstances should be accidental.

During the summer of 1910 it was observed that numbers of the crayfish taken from a pond near Columbia, Mo., were covered with the eggs of some insect. When hatched out in aquaria these were found to be a species of waterboatman.[2] The crayfish were those of a common species of the neighborhood, *Cambarus immunis* Hagen and both young and old were invested with the eggs. In well covered specimens the telson, the legs, the sides of the abdomen, and nearly the whole of the cephalothorax, including the eye stalks, and basal parts of the

[1] Forbes, *Bull. Ill. Mus. of Nat. Hist.*, I, pp. 4–5, 1876; *ibid.*, AMER. NAT., XII, p. 820, 1878.

[2] The species has been described elsewhere (*Canad. Entom.*, XXXI, pp. 113–121, 1912) as *Ramphocorixa balanodis* n. gen. et sp. and a full account of its metamorphoses given.

antennæ, were clothed with a felt-like cloak of tiny eggs each a little less than a millimeter long and imbedded in a small cup which is affixed to the carapace. The cup has been described for other species of Corixidæ which attach their eggs to stems of water plants and is not to be considered as a special adaptation in the present instance. It was found, however, that the carapace was slightly impressed for the reception of each egg cup, as if the affixing of the egg had either softened the chitin somewhat, or had taken place before the hardening subsequent to ecdysis had been completed.

In a "List of Illinois Crustacea," under *Cambarus immunis*, Forbes (*l. c.*) states that:

> About one fourth or one half the specimens taken from stagnant ponds in midsummer [in Central Illinois] are more or less completely covered above by the eggs of a species of *Corixa*, probably *C. alternata* Say, since this is much the commoner of the two species found in such situations, the other being as yet undescribed.

As the present writer has taken *Ramphocorixa* in Illinois it is highly probable that it was the "yet undescribed" species mentioned by Forbes. The same species of water bug is also found in Texas, so that it is more than likely that the distribution of the insect is coincident with that of the crayfish *Cambarus immunis*. Forbes states also that a "careful search of the weeds and other submerged objects in the ponds discovered no other place of deposit of these eggs." The writer also can testify to the same point. The waterbug in question is abundant where found, but its distribution is not general and it is not improbable that it is conditioned by the presence of the crustacean species with which it has undertaken this unusual partnership. All the Corixidæ are strong flyers and "swarm" at maturity, so that with the general similarity of habitat which exists throughout the Mississippi Valley there is no other reason why *Ramphocorixa* should not be equally as well distributed as some other species of Corixids (*e. g.*, *Arctocorisa interrupta* Say) found there.

The insect when mature, measures but 5–5½ mm. in length and a very large number of females must simultaneously participate in the egg laying so to cover an individual crayfish. No count was attempted of the eggs on any one crayfish but the number must often run well up into the hundreds.

The investiture of eggs commingled with debris certainly

renders the crayfish less conspicuous and it probably profits by the arrangement in much the same was as do various shore-crabs which are decorated with sponges, algæ or cœlenterates. Whether the water bug improves its chances against racial extermination by the adoption of such a pugnacious protector it may be too much to assume, but at any rate whatever the utilitarian value of the habit it must be of the same nature as that which obtains in the widely distributed genus, *Zaitha*. An observation of the manner of egg laying on the crayfish would be of much interest.

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DOUBLE EGGS[1]

UNDER some such caption as the above there have appeared from time to time in zoological literature various accounts of anomalous eggs, chiefly of the common hen. These have naturally elicited more or less popular interest, and various explanations have been proposed concerning them. While it is no part of the present purpose to review the history of these phenomena it may not be amiss to merely call attention to a few of the more striking titles under which they have been described. For example, Barnes ('63, '85) has described cases under the title "Ovum in Ovo"; and Schumacher ('96), "Ein Ei im Ei"; Parker ('06), "Double Hens' Eggs"; and quite recently Patterson ('11), "A Double Hen's Egg," are typical of numerous titles appearing in the literature. The chief purpose of the notes which follow is to call attention to an earlier paper by the writer ('99) and to describe subsequent facts which have come to his knowledge. The only reason for specially referring to the earlier paper ('99) is that it seems to have been wholly overlooked by later observers of these phenomena, and this is the more strange in that both Parker ('06) and Patterson ('11), to whom the journal (*Zool. Bull.*) was quite familiar and accessible, make no mention of it.

In Fig. 1, which is reproduced from the article just cited, are shown the essential features of the first case which came to my direct knowledge some time prior to the date of the paper in question. As will be noted this presents a very clear illustra-

[1] Contributions from the Zoological Laboratory, Syracuse University.

tion of that class of egg anomalies known as "ovum in ovo," and its simplest interpretation appears to be that originally given to it by Schumacher ('96), namely, that it is the result of a return of the egg up the course of the oviduct by an anti-

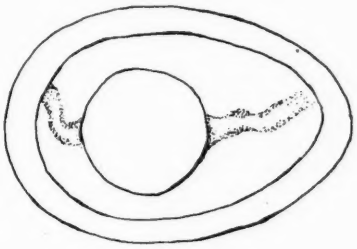

FIG. 1.

peristalsis of that organ, and then later a descent during which the egg would receive a second deposition of albumen, shell membrane and finally a second shell, giving it just the constitution shown in the figure, and described in my paper (p. 228).

In Fig. 2 is shown a case which differs in essential respects from the preceding. The egg came to my knowledge through the kindness of my colleague, Dr. C. G. Rogers, in whose father's

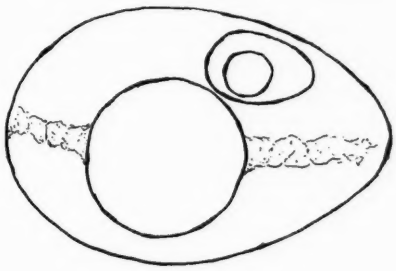

FIG. 2.

poultry yard it was produced. This egg, as will be observed, was double in a rather unusual way. Here we have as shown from the outside an egg of rather larger size than usual, but otherwise apparently perfectly normal. When broken to be used in the kitchen the anomalous internal condition was revealed. The sketch will make clear in just what this anomaly consisted.

namely, the inclusion of a miniature egg within the larger and in about the position and relation shown in the figure.

A double egg of similar character has been recently described by Patterson (AM. NAT., Jan., '11), though differing in that the anomaly comprised two fairly large eggs, as shown in his sketch (Fig. 4), while in my own specimen the inner egg was quite minute though otherwise normal. Some further discussion of these cases will appear in a later section of the paper.

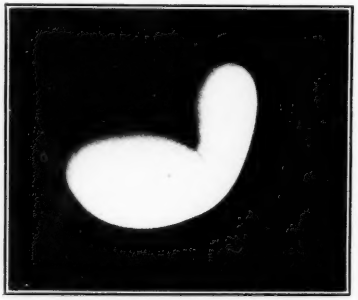

FIG. 3. Abnormal hen's egg × ½.

In Fig. 3 is shown a third anomaly differing from either of the preceeding in a very marked way. The photograph of the specimen, about one half natural size, gives a better impression of the specimen than any verbal account could do. The most striking feature is that of shape, which is rather gourd-like, and was sent to me by the father of Dr. Rogers with the rather facetious suggestion that the contiguity of the poultry lot to the garden, over whose fence hung a squash vine, might afford a clue to an explanation! The egg was laid aside for a time awaiting photography, and when later I opened it for a critical study it was found to have lost so largely by evaporation that an exact account of all its details could not be made. This may be stated, however, that in the larger end of the egg was an apparently normal yolk and normal albumen. The smaller end seemed to have had only albumen, though it was yellowish, as if there might have been yolk matter distributed through it. Of this one can not be certain, and I must leave the matter as doubtful. However, I am disposed to submit the general statement given above, namely, that the egg was comprised of about nor-

mal parts in the larger end, and the smaller probably having only albumen, its yellowish tint having resulted perhaps from the evaporating process which had taken place.

In the matter of explanation or interpretation of these facts I have little to add to what has been presented in the earlier paper or by other observers. Of the literature at my command the paper of Parker (*op. cit.*) seems to me to present upon the whole the best discussion. And I may add in this connection that Parker's paper is further valuable in its rather full bibliography of the subject. As already mentioned in connection with the account of Fig. 1, the true interpretation seems almost certainly that there cited. One has but to apprehend the essential physiological operations involved in the process of the so-called antiperistalsis to perceive just how there would result the structures present in the egg. If it should be queried why such deposition might not have taken place on the ascent of the egg by antiperistalsis as well as during the later descent, it may suffice to admit that perhaps it did occur. However, in case the return of the egg up the oviduct took place soon after its original descent the glandular structures would be in a state of exhaustion and hence capable of only slight discharge; but in either case, save only the action of the shell gland whose only effect would be to add to the thickness of the original shell, the effect would prove the same, namely, a second layer of albumen, a second shell membrane and finally a second shell just as was the case. Parker's contention as to the fact of antiperistalsis seems to me conclusive. The facts of normal eggs in the body cavity of hens, cases of which I have known, seem impossible of explanation by any other view.

The case involved in Fig. 2 is rather more complex, though not so difficult of correlation with known processes as might seem. First, let us direct attention to the minute inner egg. Such miniature eggs are fairly familiar to any one who has much to do with poultry culture or care. They are oftenest found with the first ovulation of young hens, and the writer has known of them from boyhood as pullets' eggs. They probably represent an early or premature ovulation at the beginning of sexual activity. The discharge of such minute yolk would involve only comparatively slight stimulus of the uterine glands and hence a meager discharge of albumen, etc., hence the minute size. Except in matter of size such eggs are usually normal and call for

small account in themselves. Now in the second place, let us consider what might happen at any time with the discharge of such premature eggs from the ovary. If followed soon by the discharge of a mature egg from the ovary and its normal descent it might well overtake the smaller specimen at some portion of the oviduct and easily include it within the larger mass of albumen. This, it seems to me, is probably just what happens in the majority of such cases, possibly in all. I do not overlook the still more anomalous case cited by Herrick ('99), in which the smaller included egg is in the yolk instead of the surrounding albumen. Of this Herrick offers no definite explanation; indeed, there may be some doubt as to exact facts in this case, the inclusion having been found in a cooked egg and details being uncertain.

Concerning the specimen of Fig. 3 there is little to be said. Its bizarre shape is remarkable, but here again the element of doubt as to the definite composition of the contents of the smaller end—handle of the squash—render unprofitable any attempt to discuss or speculate as to its real significance. Whether there may have been some rupture of the original yolk and the segregation of a portion in one end with the extruded part in the other may be a possible explanation; or whether some malformation of the oviduct may have been a disposing cause must remain open questions. Various egg shapes are familiar to those handling large numbers of eggs. I have myself seen many such, though none resembling the one here under consideration. That conditions of confinement, close inbreeding, or other features of habit or environment may have an influence in such matters are altogether possible. Association with unusual shapes, colors, etc., at certain times may affect domestic animals variously; *e. g.*, witness the very interesting story of Jacob's spotted cattle (!), still the contiguity of garden and poultry yard referred to above can hardly be considered as a *vera causa* in this instance!

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LITERATURE CITED

Hargitt, Chas. W. Some Interesting Egg Monstrosities. *Zool. Bull.*, Vol. II, 1899.

Herrick, F. H. 1899*a*. A Case of Egg within Egg. *Science*, Vol. IX, p. 364; *ibid.*, *b*. Ovum in Ovo. AM. NAT., Vol. 33, p. 409.

Parker, G. H. Double Hens' Eggs. AM. NAT., Vol. 40, p. 13, 1906.

Patterson, J. T. 1911. AM. NAT., Vol. 45, p. 54.

NOTES AND LITERATURE

AMERICAN PERMIAN VERTEBRATES[1]

THIS work might have been entitled Some American Permian Vertebrates. It is not a general treatise on the vertebrates found in the Permian of America, but one on a few amphibians and a number of reptiles to which the author has recently been giving his attention. The book is, however, not less valuable because of its limitations.

For a number of years Dr. Williston has been making collections from the Permian deposits of Texas. He has been studying these collections, as well as the materials secured by Cope and now in the American Museum of Natural History in New York, and the collections, now in Yale University, brought together by Marsh. Dr. Williston has found some remarkably well preserved remains and these have been most skillfully prepared by his assistant, Mr. Paul Miller; and in this book we have some of the results of their labor.

Thanks to Williston, Broili, and Case, our knowledge of the interesting animals of the Permian has been greatly increased. We seem to be justified in believing that during the Permian the principal orders of reptiles took their origin, or at most had not yet diverged far from the parent stem. It is therefore of the highest importance that every scrap of materials be studied that is likely to throw light on these reptiles and their relationships.

As it seems necessary for a reviewer to discover some errors and deficiencies, some fly in the ointment, let this duty be first accomplished.

The text is well printed and the text-figures well made and effective. Most of the plates are excellent, especially these made after drawings. Those reproduced from photographs, as Plates XXVI–XXVIII, are useful mainly in showing that the author had a sufficient basis for his line drawings. These Permian fossils are very refractory subjects for photography, being variously mottled and stained. There are, however, methods for

[1] "American Permian Vertebrates," by Samuel W. Williston, professor of paleontology in the University of Chicago. The University of Chicago Press, Chicago, Ill. Pp. 145; 38 plates and 32 text-figures. Price $2.50 net, $2.68 postpaid.

hiding such stains and giving the objects a uniform color, so that light and shade produced by the varying surfaces need not be interfered with; and it might be well to test these methods on such fossils.

The reader, at least this one, can not always determine the exact size of the animals described; for example, that of *Seymouria baylorensis*. On page 140 we are told that the figures of the plates are of the natural size, unless otherwise stated, wherefore we might conclude that the figure on Plate XXVI is of the size of nature. However, on pages 51 and 52 the figures of the same skull are explained as being one half the natural size. and they are somewhat more than two thirds the size of the skull of Plate XXVI. As the author seems not to state the size of the animal we are left in doubt.

The present writer would suggest that the important Plate V ought to have had its figures lettered so as to indicate what names the author intended to apply to the various elements. By digging in the text with sufficient assiduity the unfamiliar student may, after struggling perhaps with such expressions as "the real, so-called coracoid" (p. 57) and "the so-called true coracoid" (pp. 97, 100), determine to what parts the various terms are to be applied.

Inasmuch as Dr. Williston argues that the exact content of the terms Theromorpha and Pelycosauria and the exact relationships of the groups can not yet be determined, it would appear better to have retained Pelycosauria for the order which he calls Theromorpha, especially since Case has employed Pelycosauria in his monograph on the group. It is still more difficult to follow Dr. Williston in displacing the well-founded family name Clepsydropidæ in favor of Sphenacodontidæ; when, according to his own researches, the genus *Sphenacodon*, with great probability, does not belong in the same family as *Clepsydrops*.

Having uttered these mild complaints, it is a pleasure to recognize the value of the services rendered to science by Dr. Williston in his descriptions of *Limnoscelis paludis, Seymouria baylorensis, Varanosaurus brevirostris* and *Casea broilii*. These descriptions are based on materials so complete and so abundant that practically the whole osteology of each is known. The remains form a marked contrast with those on which Cope was compelled to found most of his work on the Permian reptiles and amphibians.

The genera *Limnoscelis* and *Seymouria* belong to the Cotylosauria; *Varanosaurus* and *Casea* to the Theromorpha. The types of *Limnoscelis paludis* are in Yale University, and were collected many years ago in New Mexico for Marsh. One specimen is a skeleton lacking only the skull, the front feet and a part of one hind foot; the other lacks only parts of the hinder feet. And all these parts are in their natural positions! What more can the paleontologist desire? Doubtless he will regret that the animal had not fallen into some pool of asphalt that had the property of preserving the flesh and internal organs. The principal skeleton described by Williston had a length of about 7 feet.

The genus *Seymouria* was originally described by Broili on two skulls obtained in Texas. Williston secured in 1910 a specimen of another species of the genus and this specimen had missing only a part of the tail; and he expects yet to secure even this. The bones are all in the closest natural articulation and are neither distorted nor compressed. This reptile was about 2 feet long.

Varanosaurus was described by Broili on a skull and part of a skeleton. Williston has secured of another species 25 skeletons, of which 6 or 8 have been recovered in greater or less perfection from the matrix. He figures a mounted skeleton and states that it measures just 44 inches in length. The head is long, narrow and pointed in front.

Casea broilii was a reptile about 3 feet in length. Its head is small, short, broad and deep. Williston presents a figure of a restoration composed of three individuals; but he thinks that in his collection there remain other skeletons. Among the peculiarities of the reptile are a large parietal foramen and a large infratemporal vacuity.

Dr. Williston presents at length the structural features that belong to the two orders Cotylosauria and Theromorpha. These are very instructive; but when we compare the two sets of characters we find that nearly all of them are either common to the two orders or of no great value. The Cotylosauria, however, possess no temporal vacuities, while the Theromorpha have one on each side. The former are said to have the lachrymal prolonged to the anterior nares; the latter not so. However, the figure, 25, of *Varanosaurus* represents this bone as reaching the nostril.

Williston evidently regards the presence of a temporal vacuity as sufficient to justify the separation of *Varanosaurus* and *Casea* from the Cotylosauria; and he may be right. His position could not be questioned if it could be shown that the presence or the absence of this feature indicated the divergence of two phyla; that the one group gave origin to descendants that retained the temporal roof intact, while the other started a line that developed one or two vacuities on each side. However, that proposition can hardly be proved as yet.

In *Varanosaurus* the temporal roof is mostly lacking and there is no lower temporal arch, differing in the latter respect greatly from *Casea*. Dr. Williston is led to discuss the value of the vacuities and arches in the classification of the reptiles. He recognizes three chief types, perhaps three chief phyla: (1) the Cotylosauria, with unbroken temporal roof; (2) the type in which there are two vacuities and two arches; (3) the single-arched type, in which there is a single vacuity bounded below by the jugal and quadratojugal. He thinks that there may be a fourth type, that in which a vacuity is bounded below by the postorbital and the squamosal. He is, however, unable to see the distinction between the two types with a single vacuity, and is inclined to believe that all single-arched reptiles have arisen from a single type. The present writer is unable to understand clearly the position taken.

Inasmuch as the temporal roof is primitively, as in the Cotylosauria, complete and composed of two series of bones, it is the vacuities which developed in them that are the important matters to consider. It seems to the writer that a single vacuity may have originated in five different ways:

1. By the development of the upper vacuity alone.
2. By the development of the lower one alone.
3. By the appearance and extension of a vacuity in the postorbito-squamosal arch.
4. By the gradual reduction of the postorbito-squamosal bar, allowing the upper and the lower vacuities to unite.
5. By the reduction of the lower arch, leaving only the upper vacuity.

The matter may be further complicated by changes in the temporal roof such as are found in some of the turtles: (1) Its lower border may be eaten away, resulting finally in a condition such as appears to exist in *Varanosaurus;* (2) the hinder border

and upper part of the roof may by degrees disappear until there is left only a narrow lower arch; and even this may waste away. Among the turtles the modifications in the temporal roof, numerous and extreme as they are, are not regarded as of great importance. It may be different, however, among the other reptiles. If so, then, as it appears to the writer, there might be five phyla of reptiles possessing in the temporal roof a single vacuity.

It is to be hoped that Dr. Williston's researches will lead to a solution of the difficult problem involved in the higher classification of the reptiles.

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FEDERLEY'S BREEDING EXPERIMENTS WITH THE MOTH PYGÆRA

INTERESTING results have recently been obtained by Federley[1] by breeding moths of the Notodontid genus *Pygæra*. Three common European species furnished the material—*P. curtula*, *P. pigra* and *P. anachoreta*.

The hybrids were not all equally easy to obtain. Numerous matings involving *P. anastomosis* were made, but no offspring were obtained. *Anachoreta* males show little inclination to pair with *curtula* females, but when such pairing occurs nearly all the eggs start developing, yet only a few reach the adult stage. On the other hand, the reciprocal mating (*curtula* male to *anachoreta* female) is easily accomplished, but produces only about 30 per cent. fertilized eggs. Of these most of the males and some of the females reach the adult stage. Thus it appears that "Paarungsaffinität" (tendency to mate), "sexuelle Affinität" (tendency toward fertilization) and "physiologische Affinität (tendency to produce fertile offspring) are independent.

One great difficulty met with was that the adult F_1 hybrids were very sterile. Only a single F_2 moth was raised, and only a few from the various back crosses (F_1 by P_1).

One of the characteristics of the species *anachoreta* is the presence of a white spot on the first abdominal segment of the caterpillar. In one of Federley's races of pure *anachoreta* there appeared, in the same brood, two caterpillars lacking the

[1] *Arch. Rass.- u. Gesellsch.-Biol.*, 8, 281, 1911. Reviewed also by M. Daiber, *Zts. ind. Abstamm.- u. Vererb.-Lehre.*, 6, 90, 1911.

spot. The mutation proved to be an ordinary Mendelian recessive. This spot is absent normally in *curtula*, and in crosses between *anachoreta* and *curtula* it does not appear in F_1, or at least is never of the full size. Its behavior in this hybrid is somewhat complicated, and more data will probably be required in order to explain it. But Federley's assumption of imperfect dominance of the same gene which behaves as a complete dominant in the *anachoreta* mutant seems hardly justifiable. The fact that the character behaves in the mutant as though due to a single factor does not mean that it must always so behave. It may depend upon the simultaneous presence or absence of several genes. If in the "spotless" mutant one of the required genes has dropped out, then the addition of that one to the complex will give the spot, and a case of Mendelian monohybridism will result. But *curtula* may be "spotless" because it lacks some other part of the required combination, in which case the behavior might be quite different from that in the case of the mutant.

When *curtula* and *pigra* were crossed, some of the F_1 imagos emerged after a pupal stage of about two weeks, while the rest hibernated as pupæ. The moths resulting from the two lots were quite different, the first (summer generation) being more similar to *curtula*, the second (spring generation) more like *pigra*. That this difference is not due to the effects of temperature is indicated by an F_2 moth reared from eggs laid by an individual of the summer generation. This moth hibernated in the pupal stage, yet resembled the summer generation. Furthermore, low temperature experiments on these *curtula-pigra* hybrids and upon *curtula-anachoreta* hybrids gave entirely negative results. Several facts bearing on this problem are given. Seasonal dimorphism is never a well-marked phenomenon in *Pygæra*, and does not seem to occur at all in the three species dealt with by Federley. From *pigra* he was unable to rear a summer generation. In the case of *curtula*, the Finnish races are univoltine, the German ones usually bivoltine. Crosses between the two latter did not give any consistent results.

The cross between *anachoreta* female and *curtula* male gives an F_1 brood which is sexually dimorphic. The males resemble their *anachoreta* mothers, and the females resemble the *curtula* father. From the reciprocal cross only males were reared. These also resembled *anachoreta*. However, Standfuss reared both

sexes but does not mention any dimorphism. Federley seems undecided as to whether this is a case of "spurious allelomorphism" (*i. e.*, sex-linkage) or a reversal of dominance due to a difference in sex (similar to the case of horns in sheep). But if, as he is inclined to suppose, Standfuss really got no dimórphism in his reciprocal cross, then this can not be a case of reversal of dominance, since if it were, reciprocal crosses would give the same results. It seems more probable that there is here a case of true sex-linked inheritance, the female being heterozygous for sex, as in *Abraxas*. Just what character is caused by the sex-linked gene is difficult to discover from Federley's account, but since this gene must be carried by *anachoreta*, let it be represented by *A*. The following formulæ, which I would suggest, in which *MM* denotes a male, *Mm* a female,[2] will then explain Federley's results:

curtula ♂ — *aM aM*
anachoreta ♀ — *AM am*

aM AM — ♂ similar to *anachoreta*.
aM am — ♀ similar to *curtula*.

anachoreta ♂ — *AM AM*
curtula ♀ — *aM am*

AM aM — ♂ similar to *anachoreta*.
AM am — ♀ similar to *anachoreta*.

The following back crosses were made:

F_1 ♂ — *AM aM*
curtula ♀ — *aM am*

AM aM — ♂ similar to *anachoreta*.
aM aM — ♂ similar to *curtula*.
AM am — ♀ similar to *anachoreta*.
aM am — ♀ similar to *curtula*.

This last mating produced only three males, which were very like the F_1 males. The next cross, and the expectation on the hypothesis of sex-linkage, is:

F_1 ♂ — *AM aM*
anachoreta ♀ — *AM am*

AM AM, *aM AM* — ♂ similar to *anachoreta*.
AM am — ♀ similar to *anachoreta*.
aM am — ♀ similar to *curtula*.

[2] I have given my reasons for adopting this sex formula for birds and Lepidoptera in another paper (*Jour. Exp. Zool.*, 12, 499, 1912).

All the males from this cross were again similar to *anachoreta*, and there was apparently a fair number of them raised. All the females belonged to the *anachoreta* type, but they are said to have been few in number.

Thus, although the classes are not all filled, because of the small numbers obtained, the results of the back crosses are in agreement with the hypothesis that we have here a case of sex-linkage of the *Abraxas* type.

One interesting point is that in the cross of *curtula* male by *anachoreta* female, from which "hundreds" of females were raised, there occurred a single female resembling the males. This furnishes another case of partial sex-linkage, in addition to the one reported by Bateson and Punnett[3] and the others which I have analyzed in another paper.[4]

In practically all of Federley's cases the offspring of back crosses strongly resembled the hybrid parents, but he explains this as probably due largely to the great mortality of the caterpillars. In only a few cases were more than three or four offspring reared from such crosses. In two such back crosses there appeared caterpillars which had entirely new colors, presumably due to recombination, but unfortunately none of these survived until the imaginal stage.

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[3] *Jour. Genet.*, 1, 293, 1911.
[4] *Jour. Exp. Zool.*, 12, 499, 1912.